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REVIEW

The Decline and Impending Collapse of the Atlantic Salmon (*Salmo salar*) Population in the North Atlantic Ocean: A Review of Possible Causes

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ABSTRACT

Adult returns to many Atlantic salmon wild and hatchery stocks of the North Atlantic have declined or collapsed since 1985. Enhancement, commercial fishery closures, and angling restrictions have failed to halt the decline. Human impacts such as dams, pollution or marine overexploitation were responsible for some stock declines in the past, but adult returns to river and hatchery stocks with no obvious local impacts have also declined or collapsed since 1985. Multiple studies have postulated that the recent widespread occurrence of low adult returns may be caused by climate change, salmon farming, food availability at sea, or marine predators but these possibilities are unsupported by stocks that persist near historic levels, loss of stocks remote from farm sites, a diverse marine prey field, and scarcity of large offshore predators. The decline and collapse of stocks has common characteristics: 1) cyclic annual adult returns cease, 2) annual adult returns flatline, 3) adult mean size declines, and 4) stock collapses occurred earliest among watersheds distant from the North Atlantic Sub-polar Gyre (NASpG). Cyclic annual adult returns were common to all stocks in the past that were not impacted by anthropogenic changes to their natal streams. A flatline of adult abundance and reduction in adult mean size are common characteristics of many overexploited fish stocks and suggest illegal, unreported, and unregulated (IUU) fisheries exploitation at sea. Distance from the NASpG causing higher mortality of migrating post-smolts would increase the potential for collapse of these stocks from IUU exploitation. By-catch of post-smolts and adults in paired-trawl fisheries off Europe and intercept adult fisheries off Greenland, in the Gulf of St. Lawrence, and off Europe have been sources of marine mortality but seem unlikely to be the primary cause of the decline. Distribution in time and space of former, legal high-sea fisheries indicated fishers were well acquainted with the ocean migratory pattern of salmon and combined with lack of surveillance since 1985 outside Exclusive Economic Zones or in remote northern regions may mean high at-sea mortality occurs because of IUU fisheries. The problem of IUU ocean fisheries is acute, has collapsed numerous stocks of desired species worldwide, and is probably linked to the decline and impending collapse of the North Atlantic salmon population.

KEYWORDS
Abundance flatlines;
IUU fisheries;
North Atlantic Subpolar Gyre;
overexploitation;
surveillance

Introduction

The abundance of adult Atlantic salmon, *Salmo salar* Linnaeus, 1758, returning to rivers around the North Atlantic Ocean has been closely watched since humans began to exploit the resource (Dunfield 1985; Mills 1989). Historically, salmon populations were so abundant writers related that fish nearly overflowed onto the riverbanks (Bigelow and Schroeder 1953; Hindar et al. 2007; Nyberg-Kallio et al. 2020). On the other hand, there have always been periods of scarcity (Huntsman 1931a; George 1982). Examination of adult returns over the last 100–200 years suggests there was a natural cycle of annual abundance (Huntsman 1931b; George 1982; Lajus et al. 2007).

In the past (pre-1985), variation of adult Atlantic salmon return abundance could often be explained by natural or anthropogenic causes, most of which were obvious or tenable to scientific enquiry. During the last 35 years, however, the characteristic, cyclic

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abundance of annual adult returns among many wild and hatchery stocks has ceased in both eastern North America and western Europe and a general, unexplained decline of annual adult returns has occurred (Hutchinson et al. 2002; Brennan and Rodwell 2008; Friedland et al. 2014; Lehnert et al. 2019; Olmos et al. 2019). Unfortunately, many stocks of Atlantic salmon are now extirpated or extinct (Parrish et al. 1998; Amiro 2003; Legault 2005; Bowlby and Gibson 2012; Forseth et al. 2017; Almodóvar et al. 2019).

Numerous impacts have been identified as the cause for the decline or loss of Atlantic salmon stocks in individual North Atlantic rivers. Before fish bypass technology was widely implemented, construction of hydroelectric or water control dams eliminated juvenile habitat, upstream migration of adults was arrested, and juveniles and adults were killed by hydroelectric turbines (Ferguson et al. 2008; Scruton et al. 2008; Lenders et al. 2016; Havn et al. 2018). During the 1960–1990 period of exploitation of salmon off western Greenland, in the Norwegian Sea, and around the Faroes, high seas fisheries were held responsible for declines of adult returns to rivers in Europe and North America (Paloheimo and Elson 1974b; Scarnecchia et al. 1991; Hindar et al. 2007). During the same period acidification of watersheds was responsible for loss of stocks in North America and Europe (Watt 1987; Hesthagen and Hansen 1991; Korman et al. 1994). Similarly, industrial pollution was the cause of adverse effects on some stocks (Saunders and Sprague 1967; Aprahamian et al. 1988; Mawle and Milner 2003), and the use of insecticides such as DDT and aminocarb impacted others (Elson 1967; Moore and Waring 1996; Fairchild et al. 1999). In other watersheds the introduction of non-endemic juveniles decimated stocks either because of introduced parasites or diseases (Johnson and Jensen 1991; Bakke and Harris 1998; Forseth et al. 2017) or genetic swamping (Ritter 1997; Karlsson et al. 2016).

More recently, numerous researchers have suggested the development of salmon aquaculture has caused negative effects and widespread losses of wild stocks from impacts on the genetic structure of wild populations (Forseth et al. 2017; Keyser et al. 2018), on wild juveniles in freshwater (Gausen and Moen 1991; Carr et al. 1997; Stokesbury et al. 2001), from mortality of wild post-smolts caused by salmon lice, *Lepeophtheirus salmonis* (Krøyer, 1837), while emigrating past salmonid farms (Butler and Watt 2003; Vollset et al. 2016; Greaker et al. 2020), by the transmission of diseases from farmed to wild fish (Garseth et al. 2013), and from escaped farm fish competing with wild conspecifics (Forseth et al. 2017). Declining condition and small size of returning 1SW and MSW adults possibly caused by a lack of preferred prey was suggested as a reason for the widespread reduction of salmon stock size due to loss of population fecundity (Bacon et al. 2009; Jonsson et al. 2016). Seal predation was blamed for decrease of adult returns since the restriction or closure of seal hunts led to dramatic increases of seal populations (Brennan and Rodwell 2008; Butler et al. 2008; Sinclair et al. 2015). Other predators, such as birds (Huntsman 1941; Elson 1962; Montevecchi et al. 2002), fishes (Hvidsten and Møkkelgjerd 1987; Beland et al. 2001; Lacroix 2014), and cetaceans (Beland 1966; Strøm et al. 2019) have also been suggested as impacting adult returns. Finally, climate change has been widely proposed as a cause in the decline of North Atlantic salmon stocks (Peyronnet et al. 2008; Jonsson and Jonsson 2009a; Trueman et al. 2012; Friedland et al. 2014; Renkawitz et al. 2015; Almodóvar et al. 2019).

It is rather paradoxical that the loss of cyclic abundance, decline in annual adult returns to wild and hatchery stocks, and the collapse of some stocks has occurred at a time when most legal, directed commercial fisheries have been progressively closed, and angling has been restricted or prohibited in many regions (Hutchinson et al. 2002; Dempson et al. 2004; Potter et al. 2004; DFO 2013). Also, during the last 60 years much has been done to improve freshwater habitat and enhance juvenile production of Atlantic salmon (Jonsson and Jonsson 2009b). Dams have been removed (Holbrook et al. 2011; Weitkamp et al. 2014), fish ways have been constructed (O'Connell and Bourgeois 1987), and pollution has been abated (Shearer 1992; Mawle and Milner 2003). Except in cases where the cause of habitat loss or stock declines are well known, such as from damming or acid precipitation; freshwater habitat in most streams has remained acceptable. In fact, in many rivers with low adult returns over a long period juvenile production remained stable until the adult population was virtually extirpated (Gibson et al. 2003; Bowlby and Gibson 2012). It is illogical that many North Atlantic watersheds which are unimpacted (little or no human habitation, undammed), have annual temperature range unaltered outside of acceptable parr survival range by climate change, have their water quality unaffected by acid rain or other pollutants, are remote from salmonid aquaculture sites, are in isolated or protected locations such as National Parks, and in which juveniles live and grow normally should have collapsed adult returns. Similarly, the loss of annual cyclic abundance and collapse of adult returns to hatchery stocks (Friedland et al. 1996; Jones et al.

2014) is difficult to explain because hatchery smolts from both European and North American sources had relatively good marine survival rates before 1985 (1.0–12.0%; Friedland et al. 1996; Jonsson et al. 2003). Since many affected salmon stocks have no known natural or anthropogenic reasons for their decline or collapse related to their freshwater habitat, the impending collapse of the North Atlantic salmon population must be largely attributed to causes occurring during the marine phase of their life cycle.

Until the last 60 years, very limited information was available on the marine life history of anadromous Atlantic salmon. Then, during the 1960s, the commercial fishery off western Greenland expanded and thousands of tagged individuals from both European and North American rivers were recaptured in that region (Christensen and Lear 1980; Jensen 1980, 1988; Stokesbury et al. 2009; Reddin et al. 2012). High-seas fisheries developed around the Faroes and in the Norwegian Sea, and research at these locations provided considerable information on marine life history (Jákupsstovu 1988; Shearer 1992; Jacobsen and Hansen 2001). In response to the occurrence of high-seas fisheries numerous research cruises were conducted in the North Atlantic (Templeman 1967; Reddin 1988; Jensen 1967; Beaugrand and Reid 2012) as well as extensive tagging studies (Reddin et al. 2012; Ó Maoiléidigh et al. 2018), studies on the levels of Cs137 in returning adults (Tucker et al. 1999; Spares et al. 2007), and studies on stable isotope occurrence in adult scales (Sinnatamby et al. 2009; Soto et al. 2018; Almodóvar et al. 2019). As a result, we now have a rather detailed knowledge of the feeding (Lear 1972; Hansen and Pethon 1985; Dixon et al. 2017, 2019), migratory behavior (Dadswell et al. 2010; Jensen et al. 2014; Strøm et al. 2018; Almodóvar et al. 2020) and genetic characteristics (Bradbury et al. 2016b, 2021; Gilbey et al. 2017) of salmon while at sea in the North Atlantic Subpolar Gyre (NASpG), the cold water complex of currents that spans the North Atlantic from Labrador to Norway north of the Gulf Stream (Figure 1; Hátún et al. 2009; Dadswell et al. 2010). With the advent of acoustic and data storage tags our knowledge of marine habitat usage by *S. salar* continues to expand (Jákupsstovu 1988; Guðjónsson et al. 2015; Strøm et al. 2020). In summary, the use of high-seas habitat for growth by anadromous Atlantic salmon was probably an advantageous evolutionary step for the species (Spares et al. 2015).

Our review will examine the numerous hypotheses that have been proposed for the trans-Atlantic decline of adult returns for Atlantic salmon during the last 35 years. Since recent management and research studies largely agree that the present decline is being caused by factors occurring in the marine segment of their life history (Jonsson and Jonsson 2004; Friedland et al. 2009; Chaput et al. 2019), and has strong spatial and temporal synchrony (Olmos et al. 2019, 2020); we will propose and examine a further possibility for marine mortality that has been relatively ignored to date. The existence of illegal, unreported, and unregulated (IUU) exploitation of fishes and other valuable marine resources is widespread and well known (Worm et al. 2006; Pramod et al. 2014; Telesetsky 2015; Link and Watson 2019; Weimerskirch et al. 2020; Witbooi et al. 2020), and should be expected in the case of Atlantic salmon (Mills 1993; Vigfússon and Ingólfsson 1993). When possible IUU high-seas fishing mortality is combined with potential mortality from climate-change stress (Clews et al. 2010; Almodóvar et al. 2019) and/or long-distance migration mortality of post-smolts (Friedland et al. 1999; Thorstad et al. 2012; Lacroix 2013; Olmos et al. 2020); we propose Atlantic salmon stocks exceed their sustainability and collapse.

The past

Once, virtually all accessible rivers and streams tributary to the North Atlantic in regions with acceptable freshwater characteristics had anadromous stocks of Atlantic salmon, and the annual runs of returning adults were treated as a sustainable resource for wealth (Netboy 1980). Stocks, of which there were approximately 2,500, existed from Portugal to Russia in western Europe, in Iceland and Greenland, and from Northern Quebec to Connecticut in eastern North America (Parrish et al. 1998; NRC 2004 NASCO 2019). Writers all commented on the abundance of the returning adults; either as large catches, (Atkins 1887), local eating habits (Netboy 1980), or prodigious annual landings (Shearer 1992). During the industrial revolution in Europe and North America salmon stocks declined or were extirpated in many rivers near human population centers because of industrial pollution (Netboy 1980; Mills 1989; Shearer 1992) and/or development of waterpower or hydroelectricity (Atkins 1887; Baum 1997; Lenders et al. 2016). Stocks less impacted by humans, however, continued to support substantial runs of 10,000 s to 100,000 s adults which were well documented by fisheries statistics (Huntsman 1931b; Elson 1975a; Shearer 1992; Erkinaro et al. 2019). At least 275 of the watersheds with salmon stocks have been studied sufficiently to provide data for a comparison of growth and life history variation across its range (Hutchings and Jones 1998),

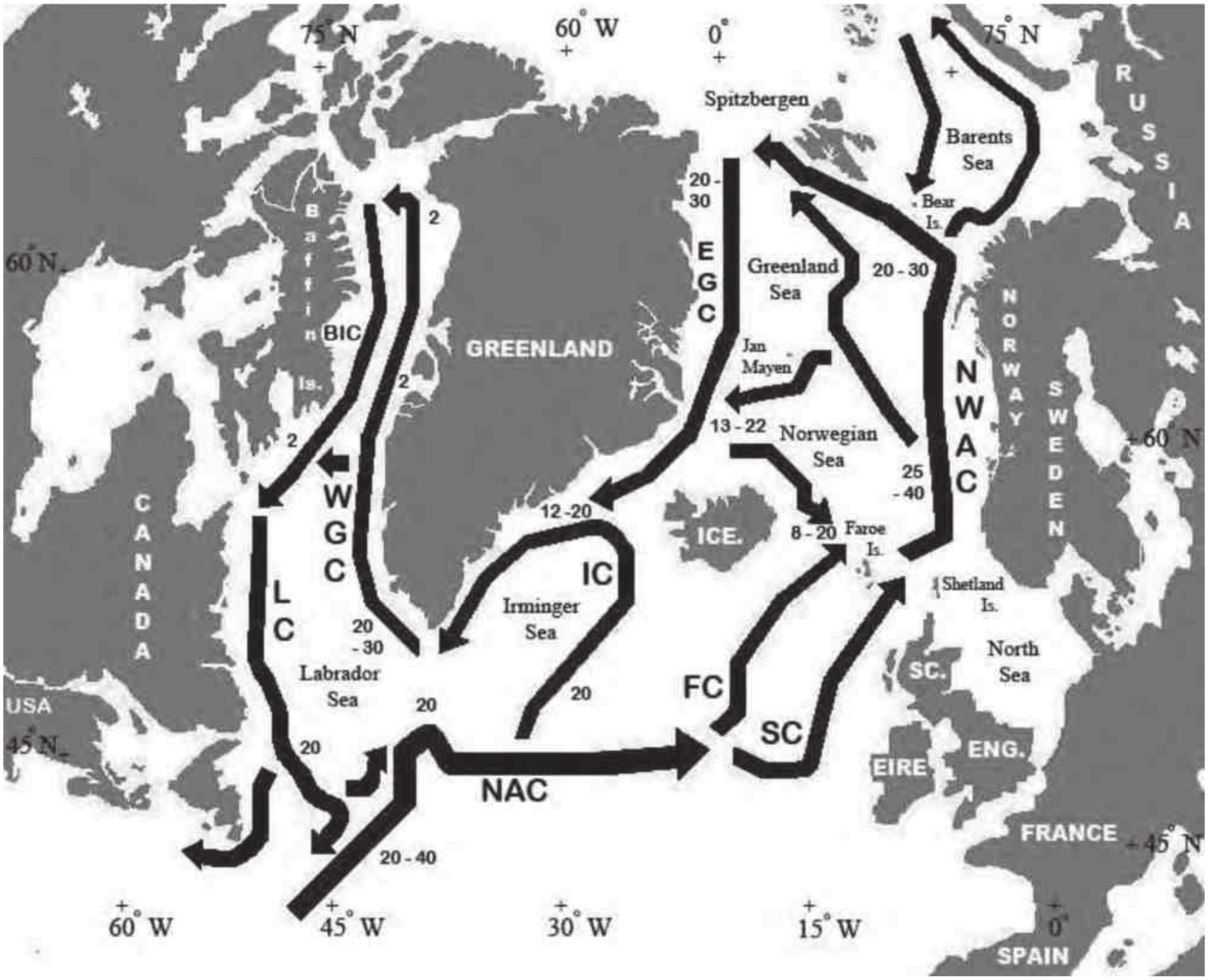

Figure 1. The current structure of the North Atlantic Subpolar Gyre used for migration by Atlantic salmon and other marine organisms (after Hátún et al. 2009; Dadswell et al. 2010). Currents depicted are WGC- Western Greenland Current, BIC – Baffin Island Current, LC- Labrador Current, NAC- North Atlantic Current, IC-Irminger Current, FC – Faroes Current, SC – Slope Current, NWAC – Norwegian Atlantic Current and EGC-East Greenland Current. Numbers by the currents are time-averaged velocities in km/d.

and numerous geographic regions and rivers have annual adult return and fisheries statistics that can be compared over long time periods (George 1982; Lajus et al. 2007).

Cyclic abundance of adult returns

One aspect of Atlantic salmon biology that was characteristic of stocks in the past, and which persists in remaining rivers with historic run sizes, is the cyclic abundance of annual adult returns. Researchers, using adult return data spanning centuries, have noted the widespread nature of annual adult abundance variability (Figure 2; Huntsman 1931b; Shearer 1992; Otero et al. 2011; Pasanen et al. 2017). George (1982) examined marine net catches for Scotland between 1790 and 1976 and described the cycles in the landings. Catches of returning adults in the White and Barents Sea drainages of northern Russia exhibited similar dynamics when landings from weir fisheries during the 17th and 18th centuries were compared with the 19th and 20th centuries (Lajus et al. 2007). To quote Houde (2016) “In monitored fish stocks, 10-fold interannual variation in recruitment is common.”

Huntsman (1931a, 1931b, 1958) was perhaps the first to seriously examine the cyclic behavior of adult return abundance of Atlantic salmon using commercial landings from Maritime Canada and the Miramichi River (Figure 3). Huntsman postulated the existence of a 9.6-year cycle of abundance similar to known 10-year fur-bearing animal cycles (Smith and Davis 1981). Berg (1935) proposed that the abundance trends in *S. salar* adult returns in Russian rivers had

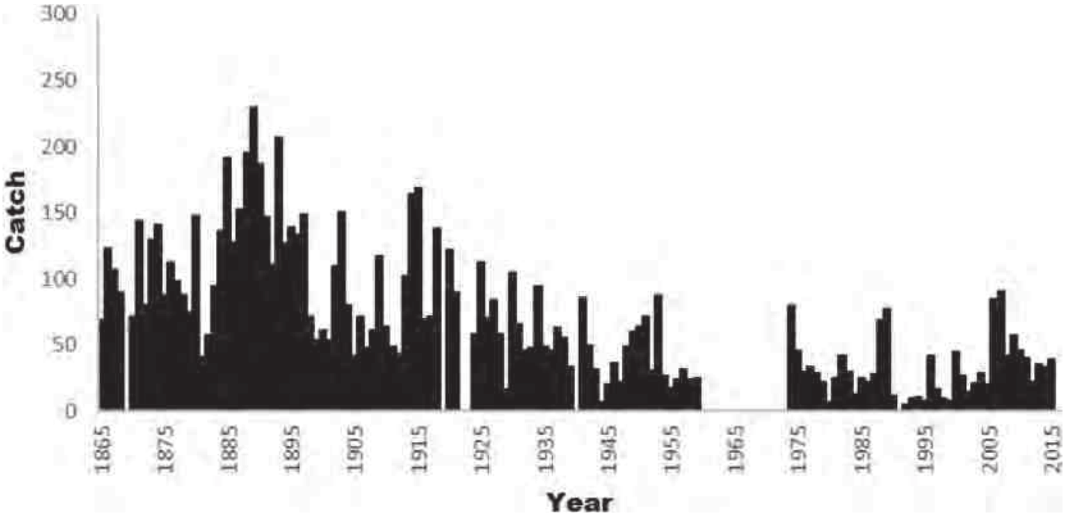

Figure 2. Annual rod catches of Atlantic salmon from the River Screebe in Ireland during 1865–2015 exhibiting a span of 150 years with cyclic annual adult returns (McDermott 1996; Tom McDermott, Marine Institute, personnel communication).

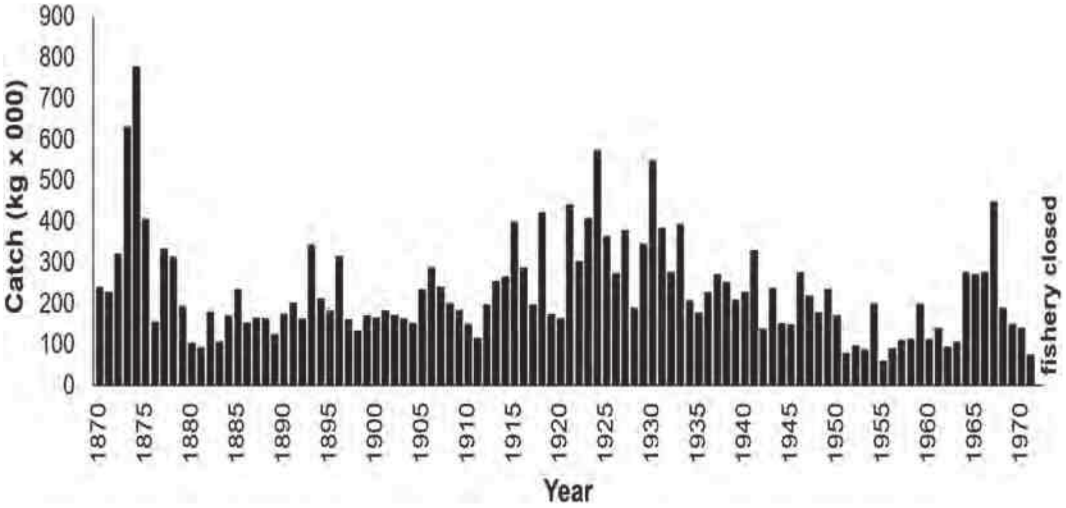

Figure 3. Commercial landings (kg x, 000) of Atlantic salmon during 1870–1871 from the Miramichi River, New Brunswick, Canada, exhibiting cyclic annual abundance of adult returns. Catch data are from Huntsman (1931b) and the Department of Fisheries and Ocean Canada Statistical Districts 70, 71 and 73 (Caddy and Chandler 1976). The commercial fishery was closed in 1972.

a 9-11-year cycle, and Niemelä et al. (2004) suggested an 8-9-year cycle for Finnish, Barents Sea rivers. A cyclic pattern with phases of 8–10 years spanning the period of 1892–1971 was observed in the commercial landings of salmon from the Saint John River, Canada (Figure 4; Dadswell et al. 1984), and angling catches in Spanish rivers from 1950 to 2010 demonstrated distinct 10-year cycles (Almodóvar et al. 2019). Finally, using Bayesian inference a 10-year cycle of abundance for adult returns to the Kola, Tuloma and Teno/Tana rivers flowing into the Barents Sea was statistically validated (Figure 5; Pasanen et al. 2017).

The cyclic abundance of annual adult returns has been reported from numerous other North Atlantic rivers (Figure 6). Gee and Milner (1980) found the total reported annual catch of salmon from net and rod fisheries in the River Wye, Wales from 1905 to 1975 had a range of ~3,000–10,000 fish that cycled over the 70-year period. Shearer (1992) examined annual rod catches in the River Thurso, Scotland which varied from 200 to 2,250/year between 1881 and 1986. Adult return abundance in many other British and Scottish rivers also exhibited cyclic adult returns (Turrell and Shelton 1993). Similarly, cyclic variation in rod catches from five rivers in the Asturias district of northwestern Spain was apparent during the period 1949–2001 (Leaniz and Martinez 1988; Perez et al. 2005), commercial catches from

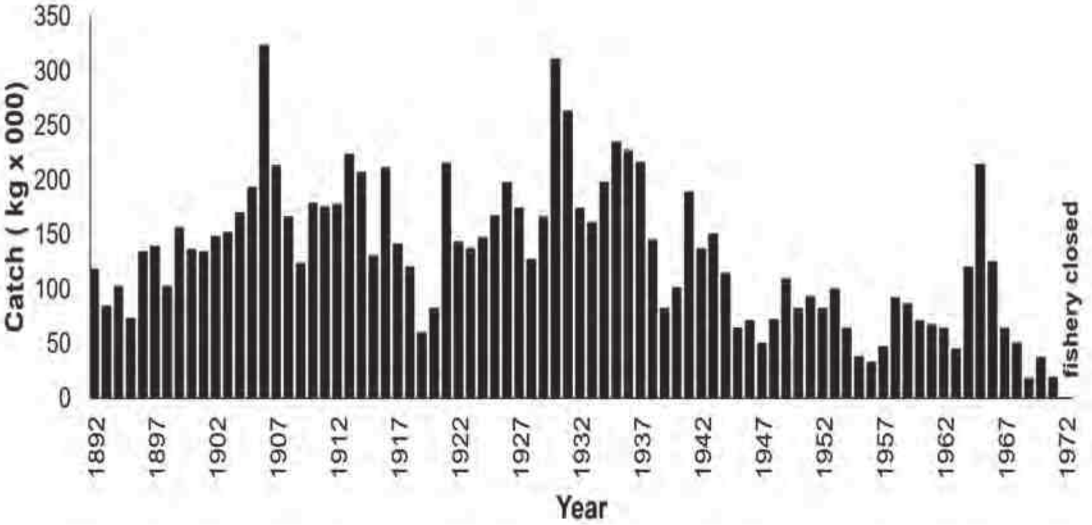

Figure 4. Commercial landings (kg x, 000) of Atlantic salmon during 1892–1971 from the Saint John River, New Brunswick, Canada, exhibiting cyclic annual abundance of adult returns (after Caddy and Chandler 1976; Dadswell et al. 1984). The commercial fishery was closed in 1972.

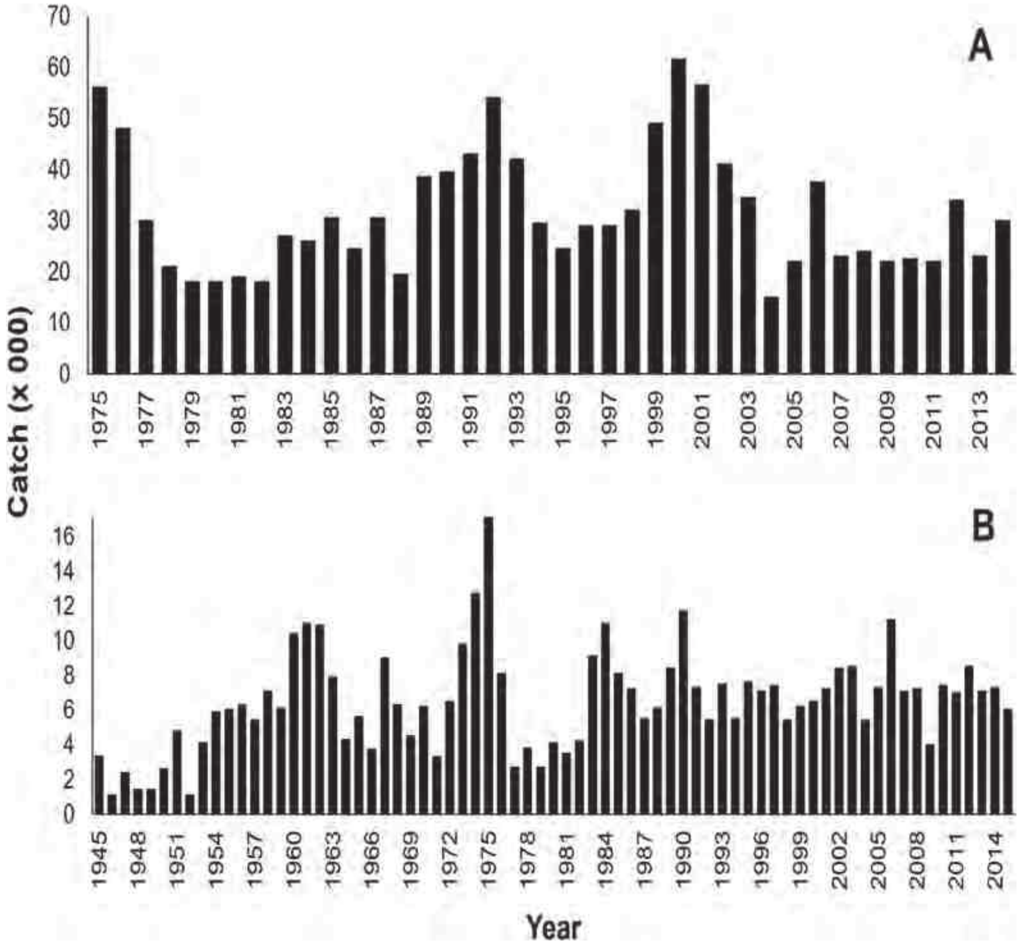

Figure 5. (Top) Commercial landings (n x, 000) of Atlantic salmon from the Teno/Tana River, Finland/Norway, 1975–2014 and (bottom) the Tuloma River, Russia, 1945–2015 (adapted from Zubchenko and Sharov 1993; Pasanen et al. 2017; Erkinaro et al. 2019).

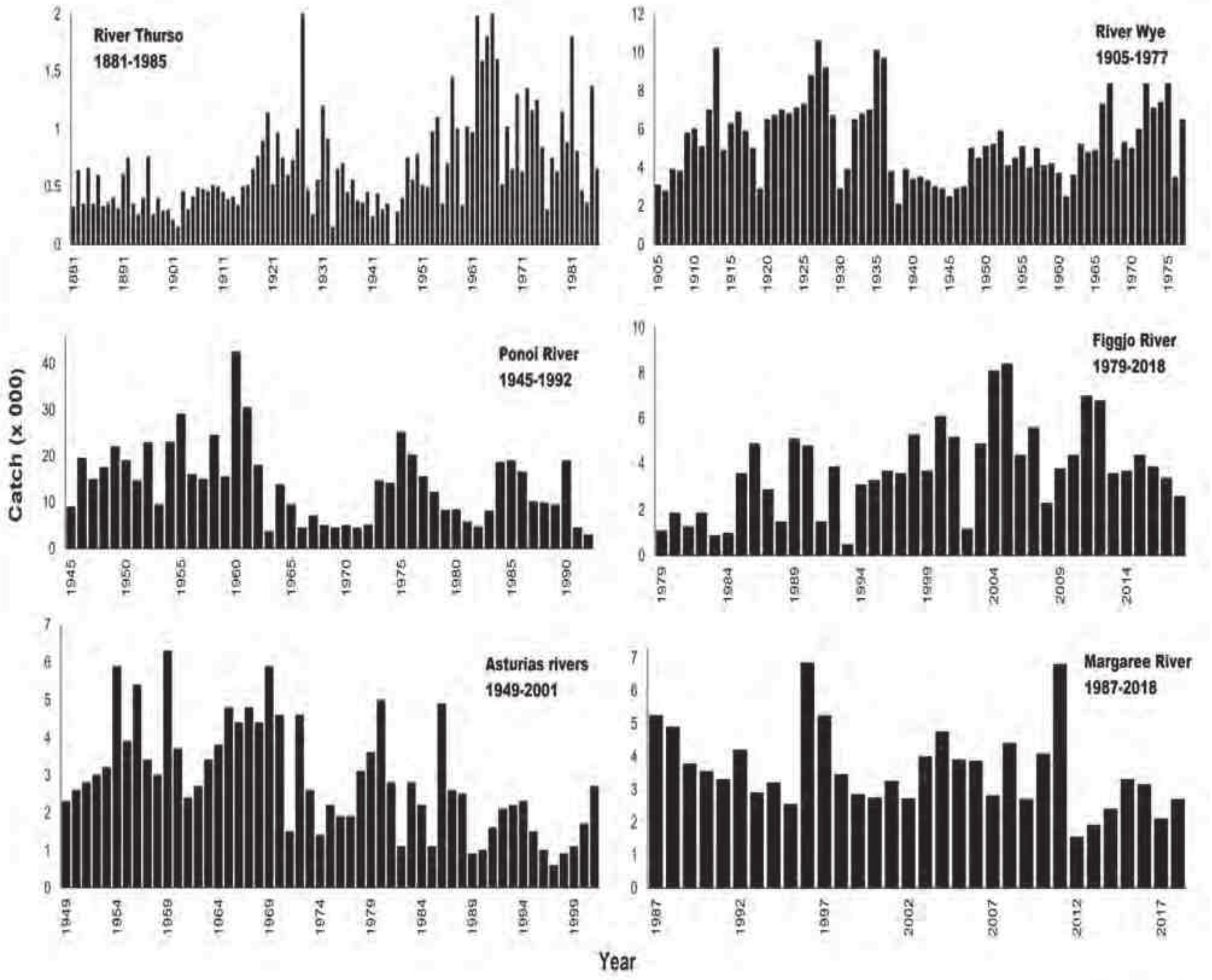

Figure 6. Annual catch (n x, 000) of Atlantic salmon from six North Atlantic locations demonstrating cyclic annual adult returns: River Wye, Wales, net and rod catches (adapted from Gee and Milner 1980); Thurso R., UK, rod catches 1881–1985 (adapted from Shearer 1992); Figgjo R., Norway, rod catches (adapted from Otero et al. 2011 and Figgjo catch records 2010–2018, Norway Map 2017); Ponoi R., Russia, commercial landings (adapted from Zubchenko and Sharov 1993), Asturias rivers, Spain, rod catches (adapted from Leaniz and Martinez 1988; Perez et al. 2005), Margaree R., Canada, rod catches (adapted from DFO 2019).

rivers on the Kola Peninsula during 1922–1992 cycled between 130 and 730 *t*/year, and the annual catch of returning adults in the Ponoi River during 1945–1992 varied from 2,500 to 42,500 fish (Zubchenko and Sharov 1993). Finally, where Atlantic salmon abundance has remained near historic levels until present, adult returns still exhibit cyclic annual returns, such as at the Margaree R., Canada (DFO 2019) and among many in Norway, the River Figgjo (Otero et al. 2011; Norway Map 2017).

Cyclic annual adult returns of Atlantic salmon from smolt releases at North Atlantic hatcheries have also been observed albeit the data cover shorter time periods. Between the early 1970s and until 1985, two sea-winter (2SW) return rates varied between 0.35 and 1.5% to the Mactaquac hatchery on the Saint John River, Canada and 0.2–1.3% for the Penobscot River, Maine, and one sea-winter (1SW) return rates to Mactaquac varied from 0.9 to 4.5% (Figure 7; Friedland et al. 1996; Soto et al. 2018). After 1985, however, annual return rates for releases from both hatchery stocks collapsed to low levels and cycling was no longer apparent in 2SW fish abundance although it persisted somewhat in 1SW fish (Figure 7; Jones et al. 2014; Anon 2019a). Similar declines in return rates from hatchery releases have become widespread in Europe (Jonsson et al. 2016; ICES 2020).

Early studies often attributed the cycles in annual adult returns and absolute abundance of Atlantic salmon to climatic variation of the North Atlantic Ocean (Scarnecchia 1984; Dickson and Turrell 2000). Recently there has been a focus on climatic variation

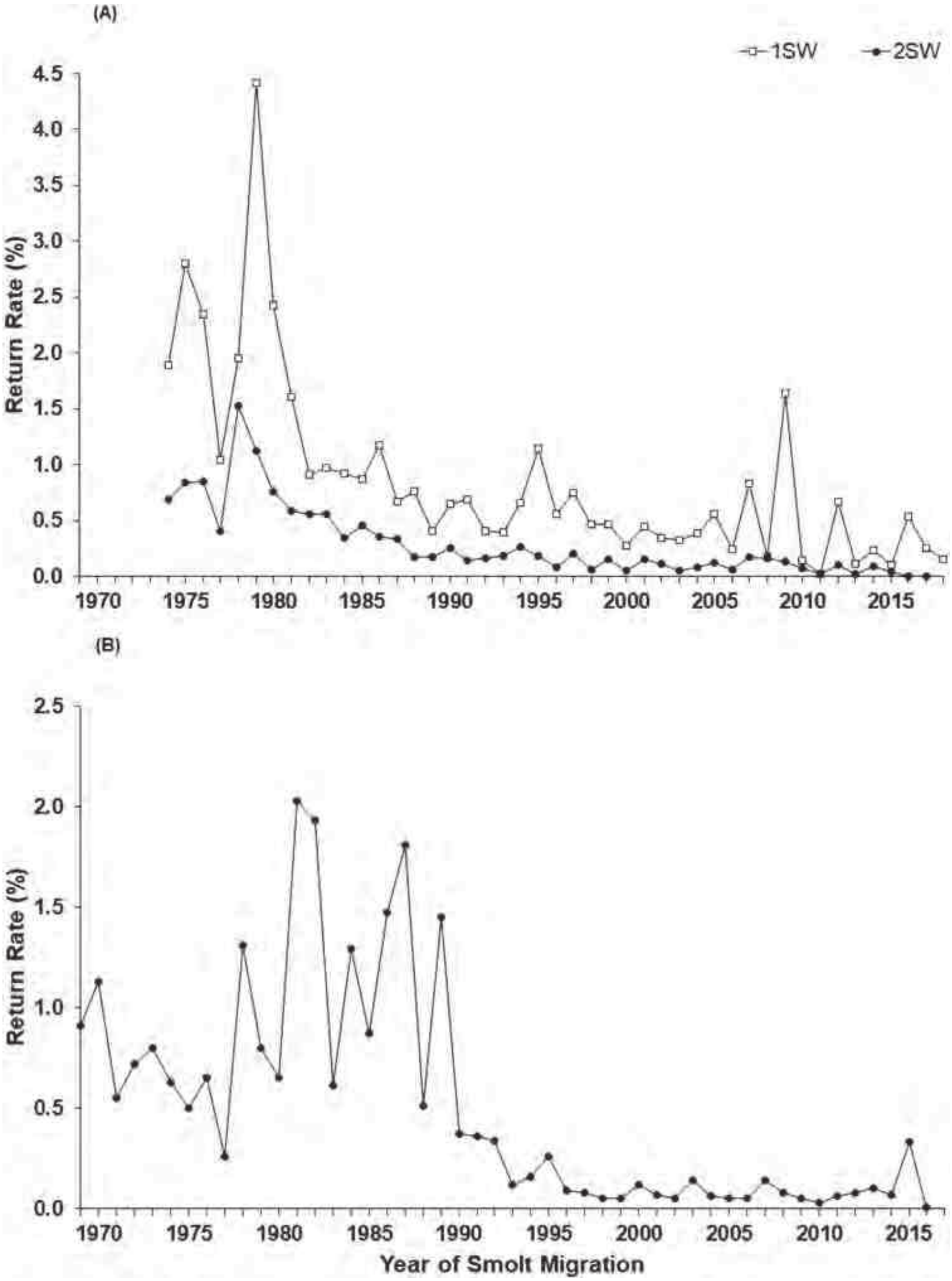

Figure 7. Return rates (%) for 1SW and 2SW adult Atlantic salmon from hatchery releases of smolts A) to the Saint John River, Canada, 1973–2018 (data from Jones et al. 2014; DFO 2020), and B) 2SW return rates to the Penobscot River, USA, 1969–2016 (data from Norman Dube, Maine Atlantic Salmon Commission, personal communication, Anon 2019a).

brought on by broadscale changes in the North Atlantic Oscillation Index (NAOI; Boylan and Adams 2006; Friedland et al. 2009; Trueman et al. 2012) or the Atlantic Multidecadal Oscillation Index (AMOI; Condron et al. 2005; Friedland et al. 2014). It would appear, however, that the effects of these phenomena may be worldwide. Birman (1979) demonstrated that the periodicity and abundance of annual adult returns of Atlantic salmon were similar to cyclic annual adult returns of Amur chum salmon, *Oncorhychus keta* (Walbaum, 1792), and proposed that climatic effects on salmonid populations were common to both the North Atlantic and North Pacific Oceans. Other studies demonstrated that climatic cycling did not seem to cause variations of adult return abundance in certain regions (Niemelä et al. 2004), although recent analysis suggests that annual cycling of returns in this same region was statistically correlated to sea surface temperature (SST) cycles in the Barents Sea (Pasanen et al. 2017). Sea surface temperature variation, rather than NAOI or AMOI cycles, has also been shown to correlate best with rate of marine growth and age at maturity (Jensen et al. 2011; Jonsson et al. 2016) and survival of post-smolts (Olmos et al. 2020).

It is beyond the scope of this review to examine either the statistical validity of the proposed cyclic phasing of annual adult returns of Atlantic salmon or its cause (Myers et al. 1998; Louca and Doebeli 2015). Rather, we argue that pronounced cyclic behavior in the abundance of annual adult returns is a characteristic of unthreatened salmon stocks and when annual cycling is no longer exhibited a stock has probably declined to an unsustainable level from the combined effects of various sources of mortality. If a hypothesis for the population collapse of salmon in the North Atlantic is robust it must explain why many rivers have lost cyclic annual adult return abundance and then collapsed while some stocks continue to exhibit cycling and persist near historic levels. We hope the logic we provide will suggest a possible answer to this question.

Decline in abundance of returning adult Atlantic salmon

It is difficult to accurately determine when the major decline in Atlantic salmon abundance began in the North Atlantic. Some workers suggest 1980 was the beginning (Kocik and Brown 2002), others suggest the mid-1980s (Dadswell 2000), and still others propose it was 1990 (Crozier and Kennedy 1993; Potter and Crozier 2000; Mills et al. 2013). It is difficult to deny, however, that a steep decline in abundance occurred from 1985 to 1995 across the North Atlantic (Figure 8). The decline in adult returns spread to rivers throughout northeastern North America and western Europe in a south to north pattern (Parrish et al. 1998) and many salmon stocks are now extirpated or extinct (Amiro 2003; Bowlby and Gibson 2012; Chaput 2012; Nicola et al. 2018).

The estimated abundance of North American 1SW salmon collapsed from 700,000 to 800,000 before 1980 to 110,000–150,000 during the 1990s, an 85% decline (Figure 8; Kocik and Brown 2002; Mills et al. 2013; ICES 2020). During the same period, estimated abundance of North American 2SW fish declined 90% from 900,000 to 100,000 and has remained near that level to the present (ICES 2020). The decline has meant that many North American stocks have persisted with adult returns that are less than the conservation minimum since 1990.

A similar decline in the abundance of Atlantic salmon returns occurred in Europe after 1985 although to date abundance persists at ~33% (Figure 8; Friedland et al. 2009; Friedland et al. 2014; ICES 2020). Among southern European stocks the decline in abundance was from 3.5 million to ~1.0 million adult returns annually (~70%), of which 1SW fish have declined from ~2.5 to ~0.6 million and 2SW fish, from ~1.0 to ~0.4 million. Among northern European stocks the decline in adult return abundance of 1SW fish was from ~1.0 to ~0.4 million, and 2SW fish from ~0.6 to ~0.3 million for a total overall decline of ~50%. At present, a greater portion of European stocks persist at levels above their conservation limits than do North American stocks (ICES 2020), however, the decline of many European stocks continues (Niven et al. 2016; Ashley 2019; Anon 2019b).

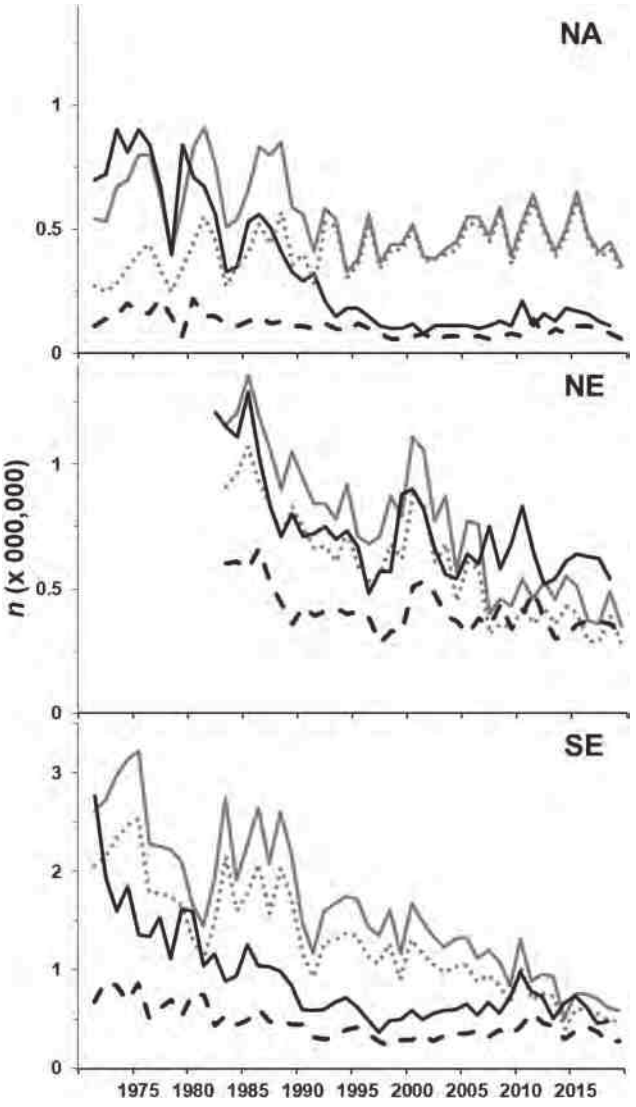

Figure 8. Estimated prefishery abundance (solid lines) and adult returns (dotted or dashed lines) of wild 1SW (gray) and 2SW (black) Atlantic salmon in millions from North American (NA), Northern Europe (NE) and Southern Europe (SE) stock complexes in the North Atlantic during 1971–2019 (adapted from Kocik and Brown 2002; Friedland et al. 2014; ICES 2015, 2020).

The loss of cyclic abundance and an overall decline in annual adult returns occurred earliest and was most pronounced for wild and hatchery stocks in southern Europe, the northeastern United States (USA) and in Canada around the Bay of Fundy (BoF) and southern Newfoundland (Friedland et al. 1996; Parrish et al. 1998; DFO 1999b; Potter et al. 2004). Smolt to adult return rates of wild stocks in the North Esk River, Scotland cycled from 1.0 to 6.9% for 1 SW and from 0.5 to 3.0% for 2 SW fish before 1985 and then declined to returns of only 0.2–1.0% for both age groups (Friedland et al. 2000). In Ireland, River Corrib 1SW adult return rates declined from 10 to 20% a year before 1990 to 4–8% a year after (Potter and Crozier 2000). In southern England adult returns to the River Frome declined sharply in 1989 and have remained at low levels since (Gregory et al. 2019) and in Spain dozens of stocks were lost completely (Nicola et al. 2018). Between 1985 and 1995 annual returns of adults from wild stocks in the inner Bay of Fundy decreased to such low levels they were declared endangered (Amiro 2003), and in the Conne River, southern Newfoundland, declines in annual adult returns of 50–60% occurred after 1988 from which the stock has never recovered (Reddin et al. 2000; DFO 2018). Among hatchery stocks in southern North America, annual return rates of smolts as 2SW adults decreased from 1.0 to 2.0% before 1980 to 0.1–0.3% after 1985, and as 1SW adults from 1.0–4.5% to 0.5–1.0% (Figure 7; Friedland et al. 1996; Jones et al. 2014; Anon 2019a).

During the same period annual returns of wild adults to rivers outside the impacted region persisted at or near their long-term levels. Estimated run sizes in the Miramichi R., Canada varied between 25,000–125,000 1SW and 15,000–37,000 2SW fish (DFO 1999). Wild, smolt to adult return rates in the River Bush, Ireland varied from 3.9 to 12.0% for 1SW and 0.4 to 1.9% for 2SW fish even with commercial exploitation rates in Irish coastal waters of 36.5 to 60.0% (Crozier and Kennedy 1993). Annual adult return abundance in northern stocks, such as at Labrador (DFO 2014), Norway (Niemelä et al. 2004; Otero et al. 2011) and Russia (Zubchenko and Sharov 1993) remained at historic levels.

Impacts on Atlantic salmon before 1985

Any review of the status of Atlantic salmon prior to 1985 would reveal that although some stocks were threatened or extirpated and authors commented on declining abundance; in general, the situation was hopeful. It was believed that if the proper steps were undertaken stocks could be revived and protected (Elson et al. 1973) or production enhanced (Taylor and Bauld 1973; Jonsson and Jonsson 2009b). The exploitation rate of many stocks at this time was as much as 50–90% annually (Huntsman 1931b; Elson 1975a; Shearer 1988), and although annual adult return rates cycled, production was relatively consistent (Figures 3, 4, and 6). The total, annual prefishery abundance (PFA) of Atlantic salmon in the North Atlantic before 1985 was estimated at 6–9 million fish (Friedland 2002).

Although many individual rivers, such as the Connecticut, Merrimac and Kennebec in North America and the Thames, Rhine, Seine and Loire in western Europe, lost their stocks of Atlantic salmon because of damming and pollution (Atkins 1887; Cuinat 1988; Parrish et al. 1998: Lenders et al. 2016); now, at many locations large scale restoration projects are underway to install fish passage and provide hatchery production to replace lost habitat (Arrignon et al. 1988; Jones 1988; Marshall 1994; Holbrook et al. 2011), alleviate pollution effects (Mawle and Milner 2003; Forseth et al. 2017), or improve existing habitat (Hartgers and Buijse 2002; NASCO 2019). The legal, high-seas commercial fishery for salmon that developed off western Greenland, around the Faroes and in the Norwegian Sea and which had depressed adult return rates in North America and Europe (Paloheimo and Elson 1974a; Scarnecchia et al. 1991; Shearer 1992), was limited after 1980. International agreements were negotiated to regulate exploitation off Greenland with quotas and restricted access, to implement a North Atlantic Salmon Conservation Organization (NASCO) closure of the Norwegian Sea fishery after 1983, and to buy out the Faroese fishery by 1991 (Vigfússon and Ingólfsson 1993; Windsor and Hutchinson 1994; Kocik and Brown 2002). Likewise, the impact of acid precipitation that had depressed or extirpated numerous salmon stocks, particularly in low pH watersheds of Canada, UK, and Norway (Watt 1987; Hesthagen and Hansen 1991), was alleviated through international agreements to decrease acid precipitation and the implementation of watershed liming (Skjelkvåle et al. 2003; Whitfield et al. 2006 Hesthagen et al. 2011), allowing some stocks to recover (Forseth et al. 2017).

Numerous other threats identified as impacting the North Atlantic population before 1985 have been either reduced or eliminated. The widespread use of pesticides (DDT, Diazinon, etc.), industrial chemicals (PCBs, etc.) and heavy metals (Hg, Cu, Zn etc.) which were blamed for declines in some stocks starting in the 1950s (Elson 1967; Saunders and Sprague 1967;

Elson et al. 1973) came under stringent regulation and/or were banned (DDT in 1968) by North Atlantic countries (Fairchild et al. 1999; Forseth et al. 2017). Most studies on predation by birds and marine mammals concluded that neither was the main causal agent of mortality for salmon (Elson 1962; Middlemas et al. 2003; Montevecchi and Cairns 2003), while stocks of some salmon prey species such as Atlantic herring, *Clupea harengus* Linnaeus, 1758, and capelin, *Mallotus villosus* Müller, 1777, which had collapsed during 1960–1980, were brought under new management regimes after which many of their populations recovered (Astthorsson and Vilhjálmsson 2002; Engelhard and Heino 2004; Hjermann et al. 2004; Obradovich et al. 2014).

Unfortunately, other impacts on the North Atlantic salmon population have since been proposed but these will be examined later. Before 1985, the number of salmon farms in the North Atlantic were few and production was limited except in Norway (Kocik and Brown 2002; Forseth et al. 2017) and the effects of farmed salmon on wild stocks were unidentified. Similarly, global climate change had yet to be fully identified and the effects of oceanic climate variance on salmon stocks were largely unstudied (Scarnecchia 1984; Turrell and Shelton 1993). Finally, the impact on salmon by marine predators or low prey abundance was relatively unsuspected (Hislop and Shelton 1993), and competition among post-smolts and other planktivorous fishes was only recently investigated (Utne et al. 2021).

Response to the decline of Atlantic salmon

The decline in the abundance of adult returns to rivers of the North Atlantic brought about a rapid change in Atlantic salmon management across its range. Prior to 1985 commercial fishing and angling were allowed in most jurisdictions. Commercial fishing was closed in the USA in 1948 because both the salmon population and commercial landings were at low levels (Bigelow and Schroeder 1953; Baum 1997), and Canada closed its commercial fishery in the Maritime Provinces in 1972 to assist stock recovery but reopened it in 1981 (O'Connell et al. 1992). In other jurisdictions in the North Atlantic, fishing continued as in the past (Mills 1989).

As abundance of the North Atlantic salmon population began its steep decline after 1985 management agencies and private groups responded. Canada reclosed the commercial fishery in the Maritime Provinces in 1985, in insular Newfoundland after 1991 and in Labrador and Quebec in 2000 (O'Connell et al. 1992; Chase 2003; Dempson et al. 2004). Reported commercial catches in Canada declined from 2,400 *t* in 1980 to 5 *t* in 1998, a hypothetical release of ~660,000 salmon adults annually for stock recovery. During the same period angling seasons in Canada were restricted or closed, daily and seasonal harvest limits were reduced, and catch-and-release angling was imposed in most regions outside of Quebec and Newfoundland and Labrador (Kocik and Brown 2002). In the United States Atlantic salmon was declared endangered in 2000 and all take was prohibited, but still by 2018 only 869 adults were reported from USA rivers (Anon 2018). In both countries, habitat improvement and enhancement efforts were increased (Davidson and Bielak 1993; Anon 2018).

In Europe, because the decline in adult returns was less rapid or extreme (Friedland et al. 2000, 2014), salmon commercial fisheries continued unaltered until the extent of the decline became widely obvious. The drift net fishery in the Norwegian Exclusive Economic Zone (EEZ) was closed in 1989 (Jensen et al. 1999). Many net fisheries off England and Wales were closed by a buy-out (Whitehead 2003; Bradbury et al. 2016b) and then completely closed in 2019 by regulatory agencies (ICES 2020). Drift net fisheries off the Irish coast were closed in 2007 and net fisheries in the estuaries of many rivers by 2010 (Jackson et al. 2013; Niven et al. 2016). The coastal net fishery off Scotland was fully closed by 2016; but not, however, before stock declines were undeniable (Ashley 2019).

Angling in Europe has always been under the control of landowners or local municipalities and as such was controlled by limited access (Netboy 1980; Otero et al. 2011), which to some extent limited overexploitation. Many angling associations are now promoting or legislating catch-and-release as a conservation measure (Niven et al. 2016). Likewise, enhancement efforts were largely undertaken by landowners or private groups such as the Atlantic Salmon Trust in UK (Mills 1991), and numerous enhancement projects have, or are being implemented (Shearer 1992; Mawle and Milner 2003; Forseth et al. 2017). There were also widespread efforts to restore salmon populations to rivers where they were effectively extinct in Denmark, Germany, Poland, Lithuania, Estonia, the Netherlands, and France (Hartgers and Buijse 2002; ICES 2019; NASCO 2019). Unfortunately, although large-scale stocking of hatchery fish has been ongoing and widespread in North Atlantic watersheds, most enhanced salmon stocks are showing little increase in abundance (Anon 2019a; ICES 2020).

The high-sea fisheries for Atlantic salmon off west Greenland, around the Faroes and in the international waters of the Norwegian Sea, because they were of mixed-stock origin (Jensen 1988; Bradbury et al. 2016b), were either closed or their quotas reduced after 1981. The quota for the Greenland fishery, which was set at 1,100 *t* in 1972 and increased to 1,265 *t* in 1981 was gradually reduced to 840 *t* by 1985. Buy outs and suspensions finally reduced the quota to ~20 *t*/year for internal consumption only (Kocik and Brown 2002). Since the harvest in this fishery ranged between 1,917 and 2,689 *t*/year between 1970 and 1975 (Scarnecchia et al. 1991; Shearer 1992) the de facto closure should have released ~570,000 salmon adults annually into the North Atlantic population after 1990 (Dadswell et al. 2010). Recently, due to negotiations between NASCO, Greenland and Denmark the annual quota and catch has fluctuated from 58 *t* in 2014 to 28 *t* in 2017 (Anon 2018).

Effective in 1984, NASCO closed the Norwegian Sea mixed-stock fishery in international waters, which should have released ~160,000 salmon adults annually into the North Atlantic population (Dadswell et al. 2010). Licenses in the Faroese mixed-stock fishery were bought out by 1991 (Vigfússon and Ingólfsson 1993; Hansen and Jacobsen 2003; Gilbey et al. 2017), which should have released another ~134,000 salmon adults annually into the North Atlantic (Dadswell et al. 2010). All in all, after closure of these high-seas fisheries and the Canadian commercial fishery there should have been an annual release into the North Atlantic population of approximately 1.5–2.0 million salmon adults a year. The question then is why, instead of rebounding because of the adults that been released from commercial fishing pressure, did many North Atlantic stocks of salmon decline steeply after 1985?

Collapse of North Atlantic stocks

The decline in adult return abundance to numerous North Atlantic stocks continued unabated through the 2000s and up to the present (Figure 8; NASCO 2019; ICES 2020). Decline of adult returns was most prevalent in rivers of the USA (Anon 2018, 2019a) southern Canada (DFO 2019; 2020), Spain (Almodóvar et al. 2019), France (ICES 2020), Ireland (Jackson et al. 2011; Niven et al. 2016), Scotland (Ashley 2019) and southern UK (Gregory et al. 2019). Adult return abundance persisted at historic levels only in the northern rivers of Newfoundland-Labrador, Norway, and Russia (DFO 2014; Forseth et al. 2017; Pasanen et al. 2017) but now many of these stocks are also declining (Anon 2019b; ICES 2020).

An example of what has happened to salmon stocks in parts of the North Atlantic is demonstrated by the recent history of two rivers tributary to the Bay of Fundy, Canada. The Upper Salmon River (USR) and Point Wolfe River (PWR) are small watersheds located in Fundy National Park with 10 and 23.3 km of accessible salmon habitat, respectively (Dadswell 1968; Alexander and Galbraith 1982). The rivers were dammed at tide head in the 1800s for lumbering purposes and their populations extirpated. After the park was established in 1948 lumbering was prohibited, the dams fell into disuse, and finally collapsed or were removed.

Upper Salmon River became accessible for salmon in 1954 and by 1963 the population in the river was estimated at 100 adults by the park wardens (Table 1; Dadswell 1968). The river has extremely clear water and fish are visible even in the deepest pools from the high, rocky banks. Reintroduction probably occurred through natural straying or from a small surviving population in the tributaries downstream of the former dam. When the first scientific surveys were conducted from 1965 to 1968 the annual spawning run was estimated to vary from 312 to 1,363 fish (Table 1). The stock was dominated by 1SW fish (64%) with a MSW component consisting of virgin, 2SW adults (6%) and mended kelts (30%), a composition similar to stocks in other inner BoF rivers (Jessop 1975; Amiro 2003). During the period of population increase a commercial drift net salmon fishery still existed in the Bay of Fundy and angling in the river was permitted after 1965. Angling catches ranged from 4 to 113 fish/year or a 1.1 to 27.5% exploitation rate (Table 1).

Point Wolfe River was not accessible to salmon until 1984 when fish passage facilities were completed at the tide water dam. Annual stocking of 42,000 fall fingerlings was conducted from 1982 to 1985 (Gibson et al. 2003).

Annual adult returns to the USR persisted at sustainable numbers until 1985 but angling was closed in 1991, after annual runs had declined rapidly (Table 1). By 1998 surveys of adult returns revealed the spawning run had collapsed to few or no fish. Small numbers of adult returns from stocking PWR were observed (few available counts) but the annual run never established a sustainable level.

Beginning in 2006 Parks Canada began a concerted effort to reestablish Atlantic salmon in both rivers. Between 2006 and 2017 a total of 968,670 parr and 1,679 hatchery reared adults were stocked in the rivers and screw-trap, smolt-run monitoring captured up to ~2,000 smolts departing the rivers annually (Table 1; Kurt Samways, University of New Brunswick;

Table 1. Selected annual adult Atlantic salmon counts, angling catch and percent of annual run, and annual number of parr or smolts sampled in the Upper Salmon River (USR) and Point Wolfe River (PWR), Fundy National Park, NB, Canada (Dadswell 1968; Parks Canada, unpublished data).

	Adults (*n*)[1]	Angling Catch[2]		Total Run Size (*n*)		Parr/Smolt Captures (*n*)[3]	
Year	USR	*N*	%	USR	PWR	USR	PWR
1963	100			100		No sampling	
1965	312			312		No sampling	
1966	600	40	6.2	640		No sampling	
1967	1,250	113	8.3	1,363		No sampling	
1968	976	109	10.0	1,085		No sampling	
1972		31				No sampling	
1973		83				No sampling	
1975		46				No sampling	
1976	400	60	13.0	460		No sampling	
1979	900			900		No sampling	
1981	145	55	27.5	200	35		
1982		63			2		
1983	540	83	13.3	623			40
1984		44					
1985	371	4	1.1	375		340	
1986	103	6	5.5	109			
1987	52			52		262	186
1989	291	20	6.4	311			137
1990	46[4]	4	8.0	50			87
1992	10			10			208
1994	15			15		70	128
1998	0			0			
2002	2			2		113[5]	
2004	4			4	2	45	
2008	3			3	9	826	137
2010	4			4	2	1,664	411
2011	3			3	41	356	62
2012	44			44	15	241	187
2013	10			10	3	100	15
2014	0			0	0	166	37
2015	1			1	3	699	104
2016	12[6](0)[7]			0	0	20	1
2017	29(6)			6	0	33	
2018	72(0)				0	2	55
2019	25(3)				3	2	115

[1] Counts during late October or early November by stream side or diver surveys after fishing season closed.

[2] Angling catch reporting mandatory with purchase of National Park fishing license.

[3] Parr only sampling 1983–1994, smolt only sampling commenced in 2002.

[4] Angling closed after 1990.

[5] Screw trap sampling conducted May 10-June 2. Captures were ~10% of smolt run.

[6] 100–300 hatchery raised adults stocked in both rivers annually, 2003–2017. 100–300 PIT tagged USR ripe adults raised at a marine aquaculture site released in USR, 2016–2017.

[7] Numbers in brackets are non-PIT tagged adults observed by divers.

unpublished data). During 2011–2019, a total of 4,534 adults from smolts captured in USR were raised to maturity at a marine, salmon farm and when ripe, released back into the river to spawn (~400–900/year). Adult releases were PIT tagged and identified in the river utilizing an antenna array or with snorkel divers using an underwater wand. Although juvenile production has increased because of this effort, as of 2019 wild adult returns (3 in USR) had still not increased substantially in either river.

One should ask, what is the problem with these Atlantic salmon stocks? Why would one river establish a sustainable population naturally during 1950–1960 only to have it disappear during 1985–1995 while the population in the other river never became established after 1985 even with enhancement efforts. Since commercial salmon fishing in the Bay of Fundy and the rest of the Maritimes was closed permanently after 1984 (Chase 2003) and there was no salmon angling allowed in Park rivers after 1990, regional exploitation cannot be blamed. Park wardens patrol the rivers extensively during the spawning run and poaching is an unlikely problem. Salmon habitat for in both rivers is excellent. Alexander and Galbraith (1982) estimated that the parr rearing area in the PWR was 170,625 m^2 and proposed that the river should develop an annual spawning run of 1,339 adults. Angling catches and adult surveys of USR during 1967–1968 found the spawning run consisted of 1085–1363 adults (Table 1).

Both rivers have a large portion of their watersheds protected by the Park and the remaining area consists of second growth forest with little or no human habitation. Fry and parr grow naturally in the rivers and successfully smoltify (Table 1). Both rivers have no industrial or municipal sewage discharges. The pH in both rivers ranges from 6.4 to 7.1 (Kerekes and Schwinghamer 1978). There are no salmon farms within 75 km of their outlets to the sea. Post-smolts from these and other BoF rivers captured seaward of salmon farms in 2001–2003 had no viral or bacterial pathogens and no salmon lice (Lacroix and Knox 2005). The multitude of enhancement efforts after 2006 have been unsuccessful. Where have all these salmon gone?

A similar fate has befallen Clyburn Brook, a small river in the Cape Breton National Park in Nova Scotia. Again, this watershed is entirely in a park and is closely monitored by wardens, who also undertake the annual diver survey. There are no commercial or recreational fisheries, and there are no aquaculture farms within 100 km of the river outlet to the sea. Unlike the Fundy Park rivers, this salmon stock consists predominantly of 2SW adults (72% of annual runs; DFO 2020). In Clyburn Brook the annual returns have declined from 100+ to 0–30 adults since 1999 (Figure 9). Where have all these salmon gone?

Regardless of commercial fishing closures, restrictions on angling, and implementation of large-scale enhancement projects across the North Atlantic, by 2020 adult returns among many Atlantic salmon stocks had collapsed to 10% or less of their long-term, historic abundance levels (Figure 8; Jones et al. 2014; Anon 2019a; ICES 2020). Famous salmon rivers such as the Miramichi in Canada and the Foyle in Ireland

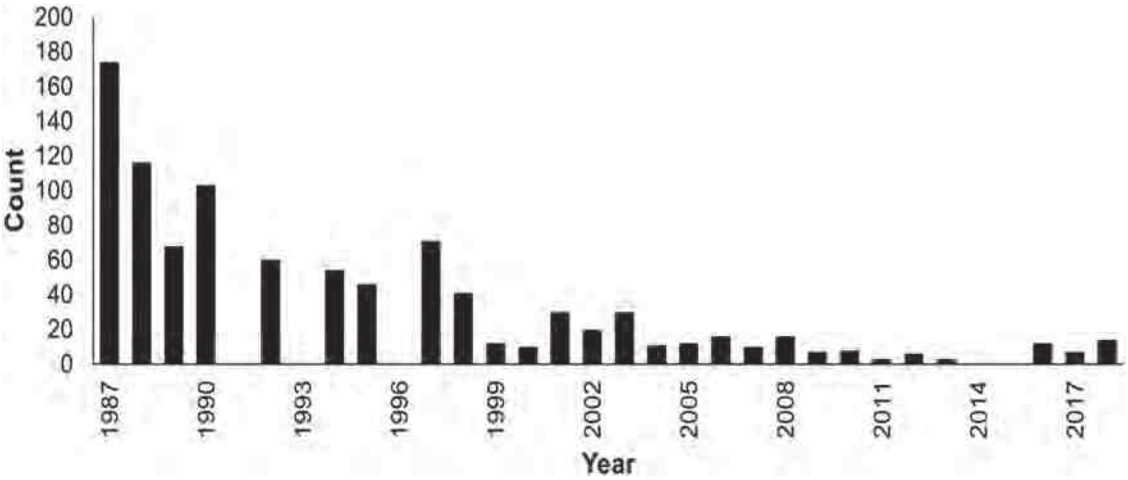

Figure 9. Annual adult returns of Atlantic salmon during 1987–2018 to Clyburn Brook, Cape Breton National Park, Nova Scotia, Canada. Annual returns were dominated by 2SW adults (72%). Data adapted from DFO 2020. Note the flatline of adult returns after 1999.

that formerly had annual adult returns of 100,000–200,000 have recorded their lowest levels since data were collected. In 1992 the adult return to the Mirimichi River was estimated at 189,647 adults, but by 2019 only an estimated 15,300 adults returned to the river (Figure 10A; DFO 1999, 2019). The total estimated adult returns to the River Foyle were over 100,000 from 1962 to 1970 (Figure 10B; Elson 1975a), but only 9,409 adults were recorded in the river by fish counters during 2015 (Niven et al. 2016). Where have all these salmon gone?

The flatline of Atlantic salmon adult returns

If cyclic abundance of adult returns in Europe and North America was a characteristic of Atlantic salmon stocks before 1985 it has since been replaced in numerous rivers across the North Atlantic by a flatline of adult returns. Among hatchery populations and stocks large and small, cyclic abundance of annual adult returns has been lost and returns have plummeted to consistent low levels.

In North America the Saint John River, which formerly had annual commercial landings in the range of 50–300 *t*/year (Figure 4), the annual return of wild adults to Mactaquac Dam has been generally less than 1,000 fish/year since 2000 (~ 3.5 *t*; Figure 11), and annual smolt-to-adult return rates of 2SW fish to the Mactaquac hatchery have flatlined to only 0.05–0.2% during the same period (Figure 7). The flatline duration for these two stocks has persisted for 30 years. Similarly, smolt to adult returns of 2SW fish from hatchery releases in the Penobscot River, Maine have seldom exceeded 0.05–0.4% since 1990 (Figure 7). The Miramichi River has been virtually flatlined since 1997 (Figure 10A) even though parr abundance during 1985 to 2010 attained the highest levels reported in the last 50 years and the mean percent habitat saturation index of juveniles increased by 200–400% after 1990 (Figure 12; DFO 1999; 2017). Paloheimo and Elson (1974b) demonstrated that there used to be a strong positive correlation ($r^2 = 0.86$) between Miramichi River smolt production and adult commercial landings. A similar positive stock-recruitment relationship ($r^2 = 0.61$) between annual smolt density and the subsequent number of angled 2SW fish was found for the Restigouche River (Chadwick 1985). In Norway, the size of smolt cohorts from the River Isma was positively related to the total biomass of subsequent adult returns (Jonsson et al. 1998). Unfortunately, for the Saint John River, parr densities are now declining in tributary streams (Figure 12), probably because the number of returning adults has persisted for such an extended period below the Conservation Limit (CL; estimated spawner number required to maintain maximum population level; ICES 2020).

Annual adult returns of wild Atlantic salmon, especially 2SW fish, in many small rivers of eastern USA and Canada have also entered a flatline state. Wild adult returns to the eight remaining down east stocks in Maine have seldom exceeded 100 adults since 2001 (Legault 2005; Anon 2019a). Annual adult return rates to the LaHave River in Nova Scotia, that used to be in the range of 1.5–8.0% for 1SW and 0.5–1.5% for 2SW fish (1,500–3,000 adults), was reduced to <0.5%/year for both groups since 2000 (<500 adults; DFO 2020). The North River in Cape Breton, NS which once sustained annual returns of 1,000–2,500 2SW fish, has been flatlined at returns of less than 300 since 1993. Adult returns to the Conne River in

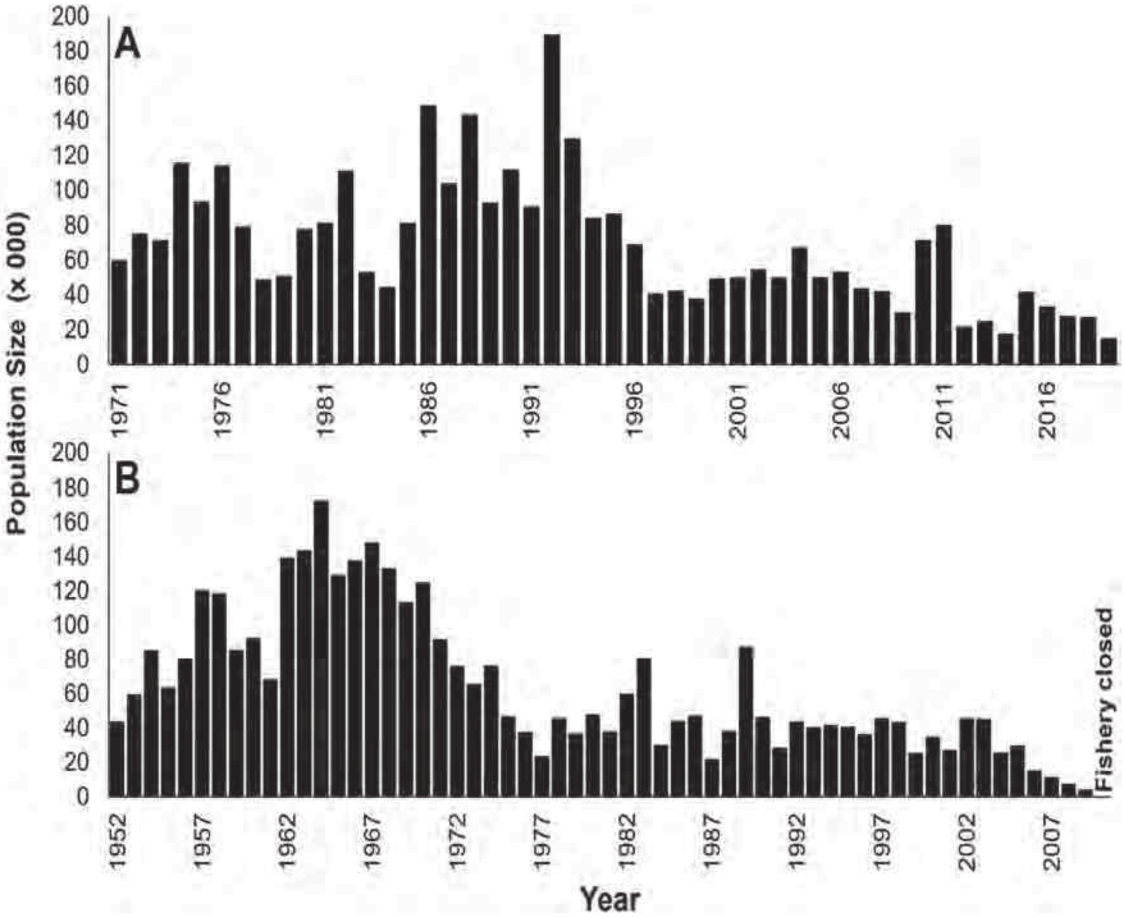

Figure 10. (A) Estimated total number of annual adult returns (n x, 000) of 1SW and 2SW wild Atlantic salmon during 1971–2019 to the Miramichi River, New Brunswick, Canada, based on capture-recapture tagging data (adapted from DFO 1999, 2019). The commercial fishery was closed in 1971, reopened in 1981 and then closed again after 1984. (B) Estimated total annual adult returns (n x, 000) of wild Atlantic salmon to the River Foyle, Ireland, 1952–2009 based on commercial landings, rod catches, redd surveys and inriver fish counters (adapted from Elson 1975a; Niven et al. 2016). The commercial fishery was closed after 2009.

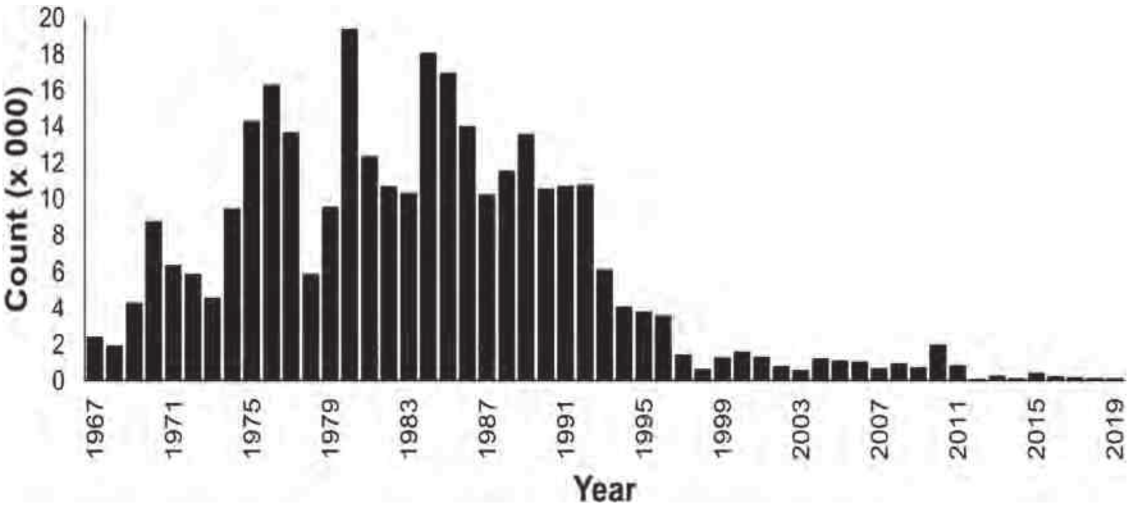

Figure 11. Adult returns of wild Atlantic salmon during 1967–2019 at Mactaquac Dam on the Saint John River, New Brunswick, Canada based on counts at the dam fish lift (DFO 2020). Note the flatline of adult returns after 1996 which declined a further order of magnitude after 2011.

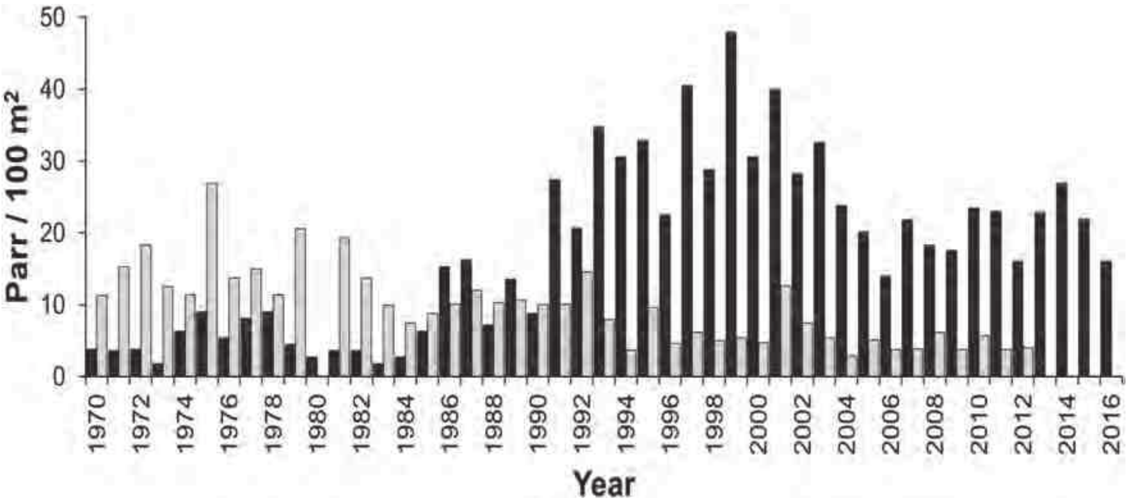

Figure 12. Estimated Atlantic salmon parr densities (parr/100m^2) for the SW Miramichi River (solid bars) from 1970 to 2016 (adapted from DFO (Department of Fisheries and Oceans) 1999a, DFO 2017), and the Nashwaak River, Saint John River basin (shaded bars) from 1970 to 2012, New Brunswick, Canada (data adapted from Jones et al. 2014).

southern Newfoundland have been flatlined since 1990 (Figure 13A) even though the annual smolt run has remained at historic levels (Figure 13B; DFO 2018) and survival of smolts in the estuary is relatively high (54–85%; Dempson et al. 2011). Conne River smolt to adult return rates have declined steadily since 1985 (Figure 13B).

The occurrence of recent flatlines for extended duration among European salmon stocks is less easy to demonstrate since the decline of adult returns began more recently. Also, numerous rivers in England and Wales are recovering from the effect of centuries of pollution (which caused flatlines in the past), and an increase in population sizes is occurring without past abundance data for comparison (Mawle 1991). In Ireland, the River Foyle entered a flatline state after 2004 (Figure 10B), and wild catches from index rivers including the Corrib and Burrishoole have flatlined since 2001 for 2SW fish and 2003 for 1SW fish (ICES 2015). Smolt to wild adult return rates in numerous European rivers with available long-term data indicate a decline has occurred in most after 1985 (Figure 14) although annual smolt runs have remained at or near historic levels (ICES 2019).

Hatchery-origin adult returns from the Corrib, Delphi and Shannon rivers in Ireland have been flatlined since 2003 (ICES 2015). The declared rod catches of salmon in “UK Special Areas of Conservation” exhibited a decline of ~50% from pre-1990 catches (Mawle and Milner 2003) and rod catches on the River Dee in Wales during 2013–2018 declined 49% from pre-2012 catches (NRW 2019). The River Frome declined sharply in 1989–1990 and adult returns have remained at a lower level since (Lauridsen 2019). Catches from coastal net fisheries in Scotland declined steeply during 2000–2010 leading to their closure in 2016 (Ashley 2019). Based on assessed stocks for 2019, out of 64 rivers in England and Wales only 13% achieved their Conservation Limit, for Ireland 28% of 128 rivers, for Scotland, 29%, and for France of 35 rivers only 3% achieved their CL (ICES 2020). It would appear the flatline of adult return abundance in southern Europe has commenced.

A flatline of adult returns was unreported among North Atlantic salmon stocks prior to 1985 except in cases where a river was dammed without fish passage facilities downstream of viable parr habitat (USA rivers, Atkins 1887; the Rhine, Lenders et al. 2016) or severely polluted (UK rivers during 1800–1950; Shearer 1992). Unimpacted stocks never demonstrated periods in the past when the loss of cyclic annual adult return abundance and a collapse of returns persisted for a period of 20–30 years (George 1982; Shearer 1992; Lajus et al. 2007). Before 1985, cyclic annual returns of adults may have declined to low levels of abundance for two or three years but never for 20 or 30 years (Figure 6).

Natural occurring flatlines of adult abundance in fish stocks caused by increased mortality during some life history stage are usually related to a major environmental regime change, an invasion or introduction of exotic competitors or random catastrophe (Lande 1993). Well-known examples of regime change are the El Nino effects off Peru causing population collapses of anchoveta, *Eugraulis ringens* Jenyns, 1842 (Schwartzlose et al. 1999), or a shift in the Kuroshio current off Japan causing Japanese pilchard, *Sardinops*

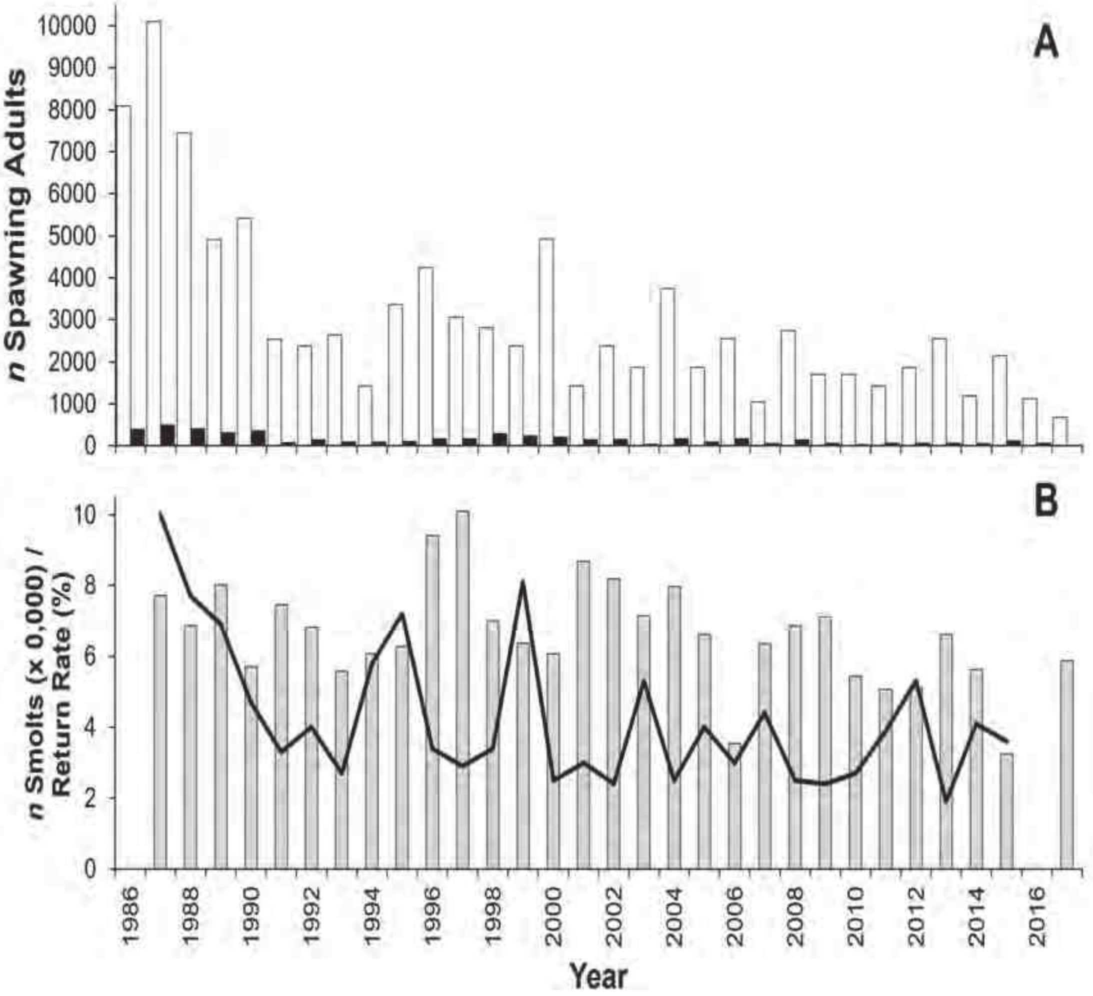

Figure 13. (A) Number of 1SW (open bars) and 2SW (solid bars) adult Atlantic salmon returns from 1986 to 2017; and (B) estimated number of smolts (open bar, X 0,000) and adult return rates (solid line, %) from 1987 to 2017 for the Conne River, Newfoundland, Canada (data adapted from DFO 2018).

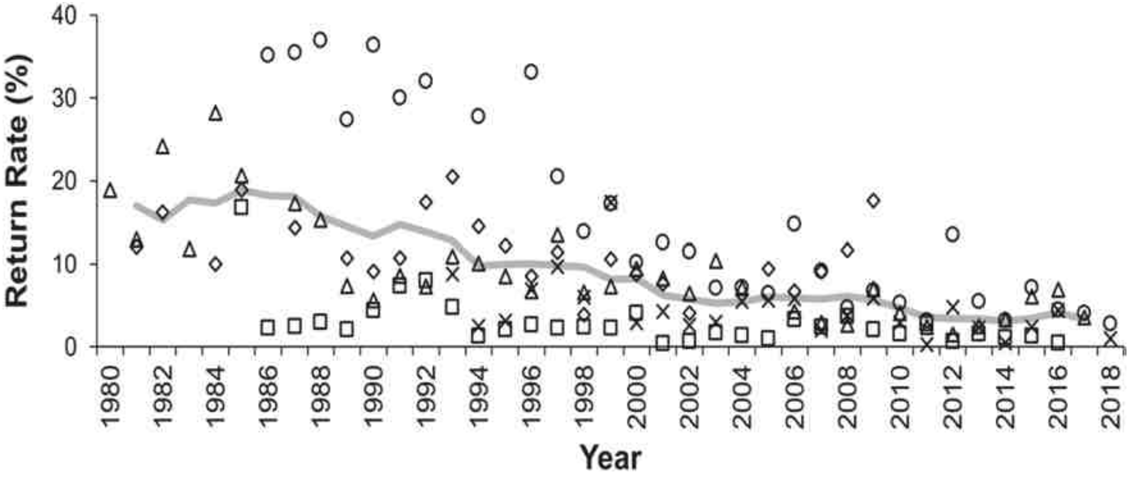

Figure 14. Return rates (%) of wild adult Atlantic salmon to southern European Rivers from 1980 to 2018, North Esk River, Scotland (◊), River Bush, Northern Ireland (o), Corrib River, Ireland (Δ), River Dee, Wales (x) and Riviére Nivelle, France (□); and three-year rolling average of all return rates (gray line). Data adated from ICES (2015, 2020).

melanostictus (Jenyns, 1842), stocks to collapse (Watanabe et al. 1995; Takahashi et al. 2009). The introduction of silver carp, *Hypophthalmichthys molitrix* (Valenciennes, 1844), in the southern USA that then invaded the Mississippi River has virtually eliminated populations of native sport fish in that drainage (Chick et al. 2020). In our opinion climate change research has failed to demonstrate a major regime change in the North Atlantic on the scale of an El Nino, and we know of no catastrophe that could have caused the collapse of some Atlantic salmon populations during the last 35 years.

On the other hand, the most common cause of the collapse of a fish stock leading to a flatline of abundance has been the result of continuing overexploitation (Hutchings 2000). The collapse of bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758), stocks in the northern and southern Atlantic (Tiews 1978; Mather et al. 1995), of Atlantic cod, *Gadus morhua* Linnaeus, 1758, stocks in the western North Atlantic (Hutchings 1996; Myers et al. 1997), and of the spring-spawning Atlantic herring stock off Norway (Engelhard and Heino 2004) are three such examples. As we develop our argument for the probable overexploitation by high-seas IUU fishing resulting in the decline and impending collapse of North Atlantic salmon population, the appearance of flatlines among adult returns to many stocks since 1985 will become an important indicator.

Decline in mean size of salmon in the North Atlantic

Another common indicator for overexploitation of fish stocks is a decline in the mean size and abundance of larger and older adults (Ricker 1975; Law 2000; Olsen et al. 2004). Reddin and Friedland (1999) demonstrated a decline in weight of Atlantic salmon in samples from North American and European stock complexes taken in the commercial fishery at West Greenland. During the period 1968–1997 observed mean whole weight in samples declined from ~3.50 kg to ~2.50 kg. Other researchers have identified similar declines in length, weight, and condition of returning salmon adults among stocks from Scotland (Todd et al. 2008; Bacon et al. 2009), Finland (Nyberg-Kallio et al. 2020) and Norway (Jonsson et al. 2016). In these latter studies, the decline was attributed to increases in SST caused by climate change, but overexploitation could also cause this effect. It should be noted that the steepest decline in mean weight of salmon samples at West Greenland occurred after 1985, during the period when annual summer SST off West Greenland was at its lowest point during the latter half of the 20th century (Jensen 1988; Jonsson and Jonsson 2009a). Additionally, the proportion of MSW fish in West Greenland samples declined from an average of 15.1% during 1981–1990 to 4.7% during 2006–2015, an unexplained loss of this portion of the population (Sheehan 2019). There was, however, no decline in mean whole weight of sampled 1 + SW fish (putative 2SW adults) at West Greenland and in fact their annual mean condition factor has increased since 2000 (Sheehan 2019).

Proposed sources of increased salmon mortality

Wild, anadromous Atlantic salmon that utilize marine habitat for adult growth have a complex life history with four stages of habitat use; freshwater growth as eggs, fry and parr in streams and lakes, estuarine and near-shore pelagic marine habitat as smolts and post-smolts, high-seas epipelagic and mesopelagic habitat as post-smolts and adults in the NASpG (except Baltic Sea stocks; Karlsson and Karlsson 1994), and freshwater rivers and streams as adults for spawning habitat (Shearer 1992; Cunjak and Therrien 1998; Hutchings and Jones 1998; Lefèvre et al. 2013). Each of these life history stages have their own sources and rates of mortality. There are thought to be three periods of higher mortality; one in the first year of life during the transition from fry to territorial parr (Elson 1975b; Cunjak and Therrien 1998; Nislow et al. 2004), the second while in the smolt to post-smolt period during downstream and estuarine migration and coastal marine passage (Baum 1997; Lacroix 2008, 2013; Chaput et al. 2019; Olmos et al. 2020) and the third from commercial and recreational fisheries during return migration of adults to spawn (Crozier and Kennedy 1993; Jensen et al. 1999; Jonsson and Jonsson 2004). The question that should be proposed is: are we able to demonstrate factors effecting Atlantic salmon stocks in the North Atlantic that have increased mortality during these periods leading to a loss of annual cyclic abundance and a flatline of adult returns?

The freshwater stage for juvenile growth of Atlantic salmon has probably been the most studied portion of its life history (Gibson and Myers 1986; Shearer 1992) but has been thought the least likely to be the period responsible for the decline of stocks during the last 35 years (Chaput 2012; Crozier et al. 2017). Research has demonstrated that climate change has led to a decline in parr survival in some stocks (Clews et al. 2010), earlier smolt runs (Russell et al. 2012), and a reduction in smolt length in others

(Gregory et al. 2019). These changes, however, were thought by researchers to account for no more than a possible 10–20% decline in adult return rates. In fact, among many stocks that have declined sharply or collapsed (Saint John, Miramichi, Corrib) parr densities and annual smolt abundance remained at or above historic levels until the collapse persisted over extended periods (Figures 12 and 13; Jones et al. 2014; DFO 2019; 2020; ICES 2020).

Since there has been little change in the freshwater habitat or survival of parr that could explain the decline and collapse of Atlantic salmon stocks, recent research has focused on estuarine and early marine stages of smolt and post-smolt survival. Most studies have shown that although survival rates can vary from 8 to 85% during estuarine and nearshore migration (Hvidsten and Møkkelgjard 1987; Beland et al. 2001; Lacroix 2008; Dempson et al. 2011; Halfyard 2014; Stich et al. 2015; Daniels et al. 2019) when post-smolts moved offshore mortality rates declined to 0.0–4.0%/day (Lacroix 2013; Lothian et al. 2018; Chaput et al. 2019). Only stocks whose watersheds are at extreme distance from the NASpG were shown to have post-smolt mortality levels that alone may have caused a population collapse (Table 2; Lacroix 2008; Thorstad et al. 2012). Additionally, Olmos et al. (2020) found that although there was strong synchrony in post-smolt survival rates among North Atlantic stocks this characteristic only explained ~40% of the variance in adult return rates which is comparable to observed annual cyclic abundance in the past (Figure 6).

An example of the possible effect that post-smolt migration distance to the NASpG has on stock abundance is demonstrated by two rivers in Newfoundland. Both rivers have been monitored since the 1980s for smolt run size and adult returns. Also, during this period, the Newfoundland commercial fishery was closed which should have benefited both populations because of reduced commercial exploitation after 1991 (Dempson et al. 2004). The salmon stock in Western Arm Brook which is approximately 520 km from the NASpG (Table 2) has experienced an increase in annual returns from 200–500 to 1,000–2,000 adults (Figure 15A) and in return rates from pre-closure levels of 0.9–4.3% to post-closure levels of 5.5–15.2% (Figure 15B). As would be expected from a commercial fishery closure annual MSW adult returns increased from 1–3 to 50–125/year. On the other hand, the Conne River which is 1,190 km from the NASpG (Table 2) has experienced a steady decline since 1986 in both adult returns and return rates. Annual adult returns have declined from 2,000–10,000 to 1,000–2,000 (Figure 13A) and return rates from 3.3–10.0% to 1.9–5.3% (Figure 13B). In both rivers, however, annual smolt production has remained relatively constant (Figures 13B and 15B). The salmon stock in Western Arm Brook, because of its proximity to the NASpG, has apparently responded to the commercial fishery closure whereas the Conne River has not, possibly because of higher post-smolt mortality at sea during migration to the NASpG combined with ongoing unexplained mortality at sea.

Table 2. Comparison among rivers of the North Atlantic Ocean in relation to their distance from the North Atlantic Sub-polar Gyre, approximate annual adult Atlantic salmon returns (2011–2018), range of 10 y wild smolt return rate, and probable population status (S = stable, D = declining, C = collapsed, E = designated endangered).

River	Distance to NASpG (km)[1]	Adult returns 2011–2018[2]	10 y return rate range (%)[3]	Population status[4]
English, Labrador	250	870		S
Western Arm, Newfoundland	520	1,250	6.0-10.1	S
Exploits, Newfoundland	350	26,750		S
Conne, Newfoundland	1,190	1,850	1.9-5.3	D
Sainte Jean, Québec	1,220	760	0.9-2.8	D
Margaree, NS	1,060	5,440	2.7-6.7	S
SW Miramichi, NB	1,250	30,000	1.7-5.5	D
LaHave, NS	1,220	120	0.7-2.0	C
Upper Salmon, NB[5]	1,950	6	0.01-0.03	C, E
Saint John, NB[5]	1,900	240	0.2-0.6	C
Nashwaak, NB	1,900	280	1.3-6.2	D
Penobscot, ME[5]	1,750	720	0.06-0.18	C, E
Naraguagus, ME[5]	1,750	14	0.7-2.2	C, E
Europe				
Tana/Teno, Norway/ Finland	100	40,000		S
Elidaar, Iceland	140		4.3-10.9	S
Figgjo, Norway	540	5,000		S
Imsa, Norway[5]	530	50	2.6-6.8	S
North Esk, Scotland	720		6.7-17.7	D
Bush, N Ireland[5]	540	700	2.8-7.2	D
Foyle, Ireland	580	10,000		D
Corrib, Ireland[5]	900		1.5-6.9	D
Dee, Wales	900	3,400	0.3-4.5	D
Tamar, England	1,220	3,900	3.0-10.2	S
Frome, England[5]	1,310	750	3.3-8.9	D
Nivelle, France	2,260	200	0.5-2.8	D
Sella, Spain	2,000	600		D
Navia, Spain	2,000	20		C, E

[1] North American distance measured to 1000 m contour off Newfoundland/Labrador and European distance measured to 1000 m contour south of the Faroes (The Times of London 1967).

[2] After: Jonsson et al. 2003; Dumas and Prouzet 2003; Niemelä et al. 2004; Perez et al. 2005; Breau et al. 2010; Niven et al. 2016; DFO 2017, 2018, 2020; Anon, 2019b; CEFAS 2020; Flávio et al. 2020; ICES 2020.

[3] After: DFO 2017, 2018, 2020; ICES 2020.

[4] S = stable, D = declining, C = collapsed, E = designated endangered.

[5] Rivers with active parr/smolt stocking programs.

We maintain, however, that higher post-smolt mortality during migration to the NASpG is unlikely to be the sole factor in the collapse of North Atlantic salmon stocks. The combination in abundance of piscine, avian and mammalian predators along the coasts of North America and Europe although in

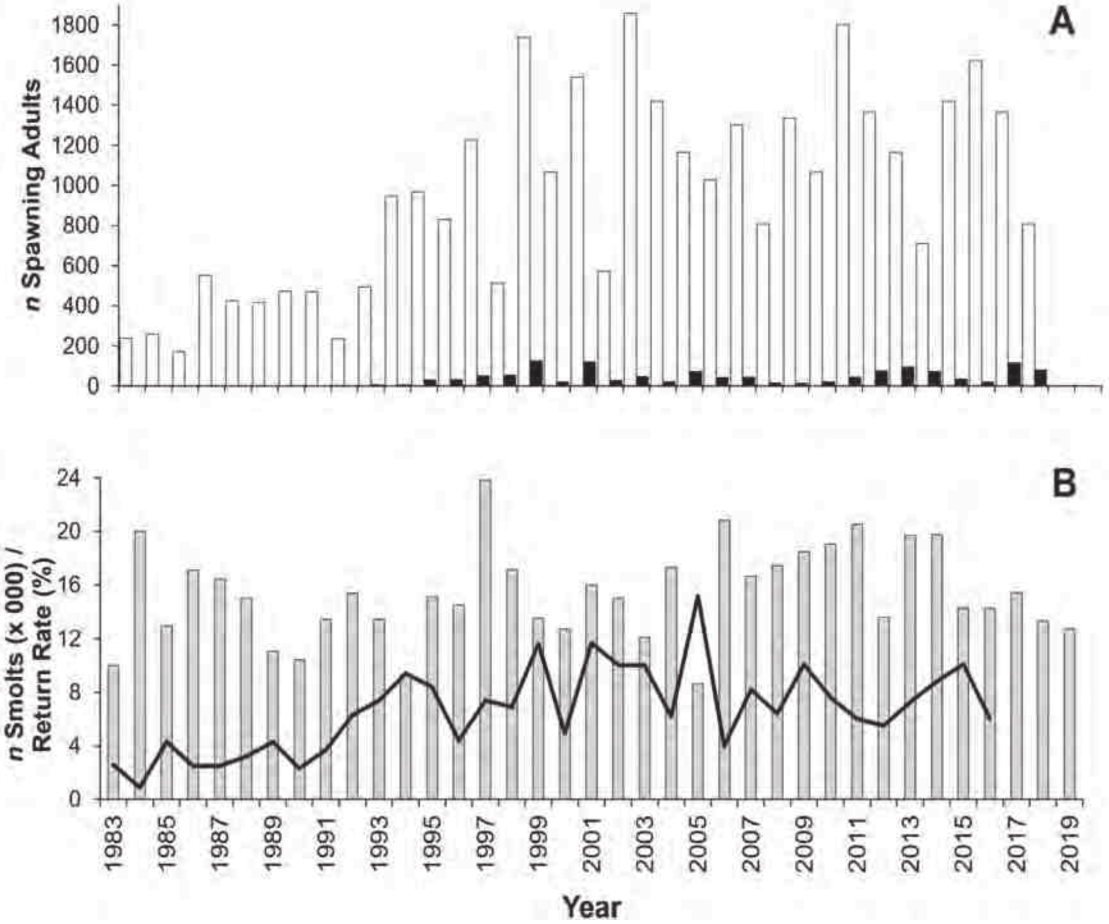

Figure 15. (A) Annual adult returns of 1SW (open bars) and MSW (solid bars) Atlantic salmon from 1986 to 2017, and (B) estimated size of annual smolt runs (shaded bar; x, 000) and adult return rate (solid line; %) from 1987 to 2017 for Western Arm Brook, Newfoundland, Canada (data adapted from DFO (2018)).

continuous flux is probably no greater since 1985 than it was in the past. Although some predatory populations such as seals and birds have undergone population increases because of protection (Baum 1997; Montevecchi et al. 2002; Butler et al. 2008; Gaston et al. 2009; Friedland et al. 2012; Sinclair et al. 2015; Stenson et al. 2020) others such as porbeagle shark, *Lamna nasus* (Bonneterre, 1788), and bluefin tuna have declined in abundance (Mather et al. 1995; Joyce et al. 2002; Horton et al. 2020; Skomal et al. 2021) resulting in a probable net impact of predation on post-smolt and adult salmon that is likely unchanged. Predation by oceanic fishes, although recently well documented (Lacroix 2014; Strøm et al. 2019), is also unlikely to be greater than in the past. When assessing the impact of mammalian predators on salmon with acoustic tags data must be considered with caution because of their ability to identify and locate fishes marked with these tags (Stansbury et al. 2014; Rub and Stamford 2020). Local fluctuations in the abundance of piscine predators like striped bass, *Morone saxatilis* (Walbaum, 1792), and Atlantic cod around individual rivers or other piscine predators in coastal regions (Hvidsten and Møkkelgjerd 1987; Friedland et al. 2012; Daniels et al. 2018; Andrews et al. 2019) are unlikely to have the overall effect of a decline in the total abundance of Atlantic salmon across the North Atlantic. Finally, compensatory effects of high natural mortality during the post-smolt migration should balance out over the life span of individual cohorts (Ricker 1975; Jonsson et al. 1998; Gibson et al. 2015) resulting in a net effect of predation on North Atlantic salmon abundance no greater than in the past.

Historically exploitation by humans probably caused the greatest mortality to adults from most Atlantic salmon stocks (Mills 1989; Shearer 1992). Prior to 1950 most fisheries were confined to coastal regions, estuaries and in rivers and exploitation was either regulated by catch limitations or by the natural rapid movement of fish past the fisheries (Potter and Dunkley 1993). Although fisheries often captured as much as 50–90% of returning adults, adult return abundance remained sustainable because of high recruitment from annual freshwater cohorts (Huntsman 1931b; Elson 1975a; Crozier and Kennedy 1993). After 1950 open ocean exploitation by drift fisheries, that could track and follow the movement of migrating salmonids with continuous exploitation (Taguchi 1957; Christensen and Lear 1980; Dadswell et al. 2010), resulted in a rapid decline of many stocks and led to international efforts to regulate and finally close most of these fisheries (Paloheimo and Elson 1974a; Shearer 1992; Potter et al. 2004; McKinnell and Trudel 2014).

The regulation and closure of Canadian, West Greenland and high-seas fisheries should have released approximately 1.5–2.0 million adult Atlantic salmon annually from exploitation. Some short-term resurgence of adult returns was observed in Canada (Paloheimo and Elson 1974a) and Europe (Windsor and Hutchinson 1994), but, unfortunately, after 1985 adult returns to natal streams and hatcheries began the steep decline particularly in USA, southern Canada, and southern European rivers (Friedland et al. 1996, 2000; Perez et al. 2005; Nicola et al. 2018). After 1990 it became obvious that PFA estimates for salmon in the North Atlantic, which had been relatively accurate before 1985, began to diverge widely from observed adult return abundance (Mills et al. 2013). By 2000 observed adult returns had declined 90% for North American stocks and 50% for European stocks (Figure 8; Kocik and Brown 2002; Friedland et al. 2009). In the case of commercial fisheries closures in Maritime Canada after 1984, in the Norwegian EEZ after 1989 and in Newfoundland after 1991 there was some recovery of river fisheries and annual adult returns (DFO 1999b; Jensen et al. 1999; Dempson et al. 2004; Niemelä et al. 2004; Otero et al. 2011). In many cases, however, the resurgence was short lived and by 2010 adult returns were once again declining or collapsed (DFO 2013; ICES 2015; Niven et al. 2016; Nicola et al. 2018; Ashley 2019). In the Tana/Teno River in northern Norway/Finland the resurgence from the fishery closure of the Norwegian EEZ was followed by a decline in adult returns that had to be addressed by further catch restrictions in the river during 2017 (Erkinaro et al. 2019; Anon 2019b). Where have all these salmon gone?

Potential IUU Atlantic salmon fishing in North Atlantic

When NASCO was established, no provisions were provided for surveillance outside the EEZ of signatory nations (Figure 16; Windsor and Hutchinson 1988). This oversight left a significant gap in enforcement of the Convention and opened international and remote regions of the NASpG for potential IUU exploitation by high-seas fishers. Large areas of the Labrador Sea, the Irminger Sea, Norwegian Sea, Barents Sea, Greenland Sea, Fram Strait, Denmark Strait and Baffin Strait, all of which are occupied by Atlantic salmon at different times of the year, were available for IUU exploitation (Figure 16; Jensen and Lear 1980; Rikardsen et al. 2008; Dadswell et al. 2010; Strøm et al. 2018; Bradbury et al. 2021). As global climate change warms the Arctic, ice free zones and temperatures selected by salmonids are extending northward (Fortiér et al. 2006; Nielsen et al. 2013; Jensen et al. 2014; Knies et al. 2014; Dabrowska et al. 2020). Since Atlantic salmon is an epipelagic fish, it like other pelagic organisms would respond rapidly to warming temperature and extend its range into remote northern regions (Hátún et al. 2009; Bilous and Dunmall 2020; Ehrlich et al. 2020), where there is little or no surveillance. Fishers know full well the migration pattern and the ecological preferences of salmon and would be expected to respond to changing migration patterns quickly (Dadswell et al. 2010).

The presence of IUU fishing for salmon in the North Atlantic was either speculated or observed to some degree after NASCO was formed (Shearer 1992; Mills 1993; Vigfússon and Ingólfsson 1993; Hindar et al. 2007), but no significant steps other than diplomatic efforts concerning flag of convenience vessels were taken to prevent IUU activities. When high-seas fisheries for salmon were closed in the North Pacific Ocean after 1988 (McKinnell and Trudel 2014) wide-spread surveillance of the offshore salmon habitat using ships and aircraft was implemented by the North Pacific Anadromous Fish Commission (NPAFC) composed of USA, Canada, Japan, South Korea, and Russia (Radchenko 2020). During 2019 the coordinated enforcement efforts of NPAFC member countries covered significant portions of the convention area with over 430 hours of aircraft and 260 ship-days to deter and interrupt IUU fishing (Anon 2020). While surveillance was only one step taken to manage the conservation of Pacific salmon the overall result has been successful maintenance of high abundance among many offshore migrating stocks (Ruggerone and Irvine 2018). We suggest the impending collapse of the North Atlantic salmon population may well be from IUU fisheries.

Unfortunately, it is difficult to prove IUU fishing for salmon in the North Atlantic outside the EEZ

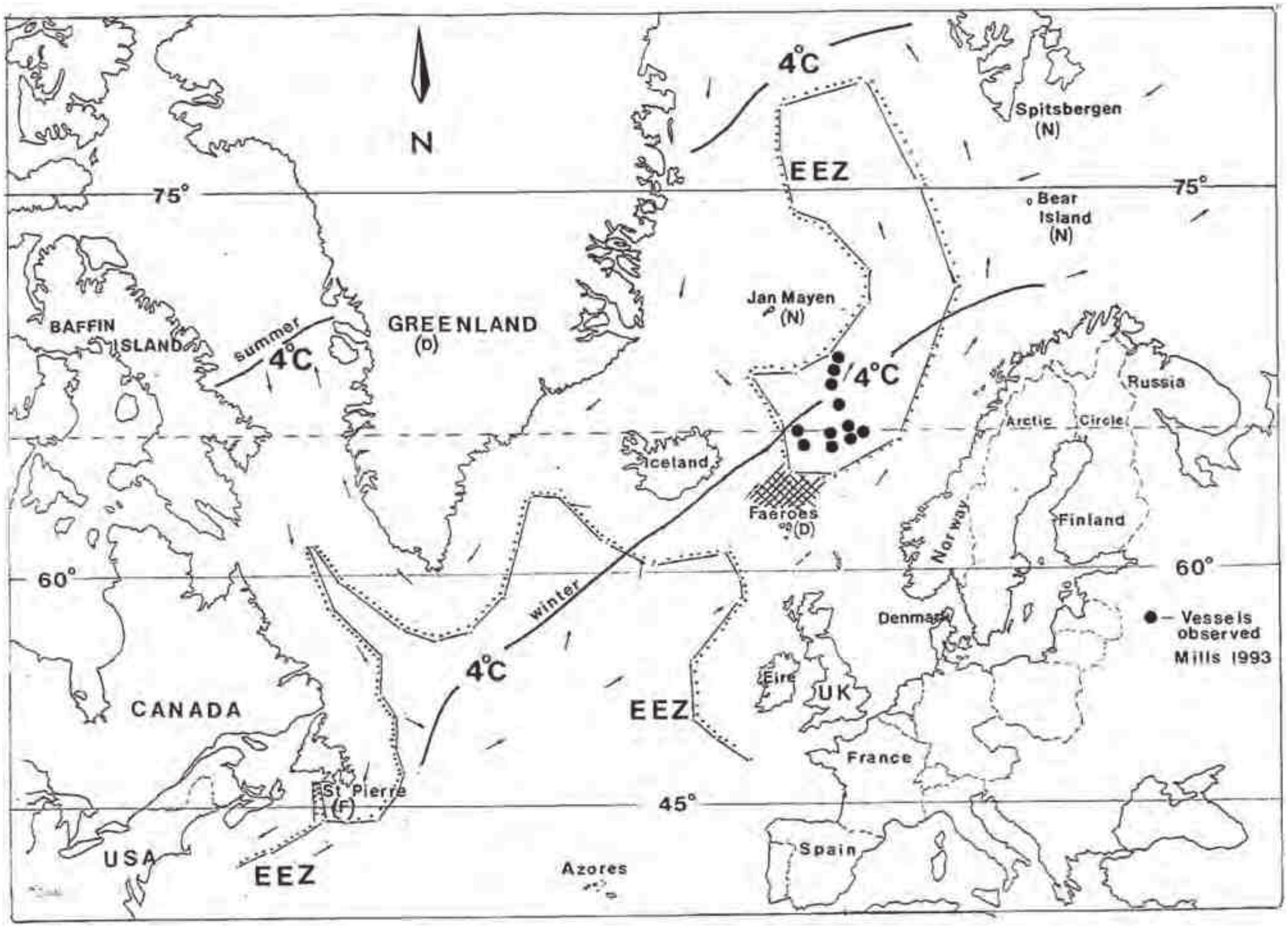

Figure 16. Atlantic salmon habitat in the North Atlantic Ocean in relation to currents of the North Atlantic Subpolar Gyre (arrows), approximate northern (summer) and southern (winter) limits of the 4 °C Sea Surface Temperature isotherm, and EEZ areas of Canada, Greenland (Denmark), Faroes (Denmark), Iceland and Norway. Black dots are where IUU fishing vessels were observed in the international (banana box) zone of the Norwegian Sea (Mills 1993). Crosshatching is the former area of the Faroes long-line fishery (Jákupsstovu 1988).

zones of NASCO signatory nations. There are no records accessible to researchers or lists of intercepted vessels such as those available from South Asia and the North Pacific (McKinnell and Trudel 2014; Funge-Smith et al. 2015; Radchenko 2020). The only path is to hypothesize that IUU activity exists based on observations of biological characteristics of the declining and collapsed Atlantic salmon stocks and compare these to other known cases for IUU over-exploitation of marine resources, many of which were hidden from public view for long periods (Anon 2009; Ivashchenko and Clapham 2014). The United Nations realized that driftnet fishing was unsustainable and adopted a resolution to ban it worldwide (Burke et al. 1994). Unfortunately, regional fisheries commissions need to enforce the ban.

Illegal, unreported, and unregulated exploitation of marine resources became a widespread fact during the 20th century (Worm et al. 2006; Anon 2009; Pramod et al. 2014; Funge-Smith et al. 2015; Telesetsky 2015). Large fishing fleets from Japan, China, Spain, Norway, Russia, and vessels carrying flags of convenience exploit invertebrates, fishes, and cetaceans throughout the global oceans (Yablokova 1994; Rosenthal 2008; Clarke et al. 2009; Kindong et al. 2020; Rodríguez et al. 2021). Many of the species captured are exploited unsustainably because they represent desired food items or needed industrial products (Horodysky et al. 2016; Link and Watson 2019; Witbooi et al. 2020). Bluefin tuna particularly are pursued in all oceans because of their high value in Japan and South Korea, and all stocks world-wide are now depleted (Mather et al. 1995; Horodysky et al. 2016). Sharks are targeted for their fins by Chinese and flag of convenience vessels (Worm et al. 2013). Spain exploits white fleshed fish worldwide for freezing and sale in Europe (Rosenthal 2008) and Norway and other EU countries pursue blue whiting, *Micronesistius poutassou* (Risso, 1827), and euphausiids in the North Atlantic and the Southern Ocean to supply the large-scale salmon aquaculture industry (Forseth et al. 2017). Numerous national vessels and those with flags of convenience exploit orange roughy, *Hoplostethus atlanticus* (Collett, 1889), over open-ocean seamounts worldwide (Francis and Clark 1998) and other desired species such as Patagonian toothfish, *Dissostichus sleginoides* Smitt, 1898, wherever they can find them (Witbooi et al. 2020). Abalone are a favorite IUU take in the southern hemisphere (Witbooi et al. 2020) and squid worldwide (Park et al. 2020). Perhaps one of the most disastrous IUU exploitations was the world-wide whale harvesting by Soviet Russia during 1945–1976 that was unknown until after the collapse of the Soviet government in 1989 (Yablokova 1994; Ivashchenko and Clapham 2014). This exploitation occurred while the Soviet government was signatory to the International Whaling Commission moratorium on whaling!

Because of its desirability as food, illegal and unregulated exploitation of Atlantic salmon populations has been a long-standing problem both in freshwater and at sea. Poaching and overexploitation in rivers have been a serious problem throughout its range for centuries (Atkins 1887; Bigelow and Schroeder 1953; Netboy 1980; Shearer 1992). Illegal fishing practices and overexploitation in coastal seas is well known and has plagued most fisheries jurisdictions (Dunfield 1985; Mills 1989). There is little reason not to expect that IUU overexploitation might be occurring in the North Atlantic outside Exclusive Economic Zones and in remote regions. Shearer (1992), Mills (1993) and Vigfússon and Ingólfsson (1993) reported IUU fishing for salmon from Greenland and in the international zone of the Norwegian Sea (Figure 16). This IUU activity was observed by Icelandic and Norwegian maritime patrol flights during 1989–1992 and the vessels concerned were Scandinavian vessels flying flags of convenience from non-contracting NASCO parties (Panama and Poland; Mills 1993). Diplomatic approaches were made which led to regulations against such activity by Panama and Poland. Unfortunately, NASCO maintains that IUU fishing for Atlantic salmon on the high seas was no longer a problem after 1994 (FAO 2003). Based on the mystery concerning the high mortality of Atlantic salmon while at sea we suggest this conclusion is incorrect. Further, while most Fishery Commissions worldwide (NPAFC, etc.) maintain and contribute to the Combined IUU Vessel List (CIUUVL 2020), NASCO does not.

We suggest it is the responsibility of the appropriate fishery commissions to provide surveillance and investigate the possible existence of an IUU drift fishery for Atlantic salmon in the North Atlantic. During the period from 1968 to 1975, 90–100 vessels largely from Greenland, Denmark, Norway, and the Faroes participated in the drift fishery off West Greenland and landed 1,127–2,689 *t* of salmon annually (Table 3; Jensen 1988; Scarnecchia et al. 1991; Shearer 1992). Partitioned over the fleet, each vessel could have captured ~ 22 *t* annually during the season between early August and late September (Christensen and Lear 1980; Sheehan 2017). Since the West Greenland fishing period was only about 40–60 days long (Christensen and Lear 1980), an individual IUU vessel fishing offshore in the NASpG for half a year (180 days) could conceivably capture up to 100 *t* of salmon. Based on this calculation it would require only 20 vessels to produce the same catch as the former West Greenland fishery and 30 vessels to replace the former exploitation of the West Greenland, Norwegian Sea and Faroes fisheries combined. If the vessels are capable of fishing for a longer period annually fewer vessels could produce the same or greater catch especially if they transshipped catches at sea (Pramod et al. 2014; Ewell et al. 2017). A total of 20–30 vessels would have little difficultly going unnoticed outside the EEZ of signatory nations in the Labrador or Irminger seas or in the remote regions off the north, east and south coasts of Greenland (Figure 16), especially with the lack of surveillance since 1984. In fact, Japanese companies have maintained a fleet of high-seas vessels in the North Atlantic with little public notice since 1960 to capture squid and large pelagic fishes (tunas, marlins, etc.; Yokawa and Uozumi 2001). Approximately 120 Japanese vessels a year utilize St. John's, Newfoundland for supplies, fuel, and crew changes (M. Takimoto; ships chandler, St. John's, NL; personnel communication). It is well known and profitable for many that IUU fleets use numerous available ports worldwide for resupply and personnel exchange (Rodríguez et al. 2021).

Table 3. Number of vessels, annual catch, and annual catch vessel^{-1} for Atlantic salmon in the Greenland commercial drift fishery during 1968-1975 (after Christensen and Lear 1980).

Period	Vessels #	Annual Catch *t*	Annual Catch Vessel^{-1} *t*
1968–1971	100	2,043	20.4
1972–1975	90	2,100	23.3

Vessels were from Denmark, Norway, Sweden, and the Faroes.

Apparently, some entity is providing wild salmon to the international smuggling market. Sackton (2018) reported that 1,000 *t* of contraband Atlantic salmon (not farmed), identified as being from Canada and

Norway, was intercepted by Chinese authorities while crossing the Vietnamese border. On the other hand, China appears to be importing IUU salmon from Russia (Pramod et al. 2014).

For several reasons, we suggest that IUU fishing for Atlantic salmon probably occurs in the Labrador and Irminger seas and perhaps inside and outside the EEZ of signatory nations in remote regions of the NASpG off southern, eastern, and northern Greenland and possibly in the northern Barents Sea (Figure 16). It is less likely that much IUU fishing has continued in the international area of the Norwegian Sea by flag-of-convenience vessels after steps were taken to prevent it (Mills 1993; Hindar et al. 2007), and because this region has very active pelagic trawl fisheries which would make detection of IUU vessels more probable (Kroodsma et al. 2018; Rybicki et al. 2020). Fishing by IUU vessels flagged in other counties, however, such as Belize or Honduras that are not signatory to NASCO or included in diplomatic agreements could still be operating there (Potter and Dunkley 1993). Drift fishers could also access the same salmon resource by fishing inside or outside the Greenland or Norwegian EEZ in the Denmark and/or Fram Straits and off southern Greenland during spring and early summer when environmental conditions of the NASpG in this region are optimal for salmon, and the main run of both North American and European stocks in the Irminger and Greenland seas migrates through the region (Figure 1; Jensen 1967; Jensen and Lear 1980; Dadswell et al. 2010; Strøm et al. 2018). Interestingly, this region exhibits elevated levels of transshipment activity for reefers as determined by Automatic Identification System (AIS) detections, which indicates they are probably accessing IUU and/or other fishing vessels for rapid shipment to market (Boerder et al. 2018; Miller et al. 2018).

High AIS detection rates also indicate drift fishers are exploiting the central region of the Labrador Sea during summer and autumn between latitudes 55 and 60°N (Figure 16; Kroodsma et al. 2018). Catch rate of Atlantic salmon by research vessels in this region during late summer and autumn were similar to West Greenland during summer (Reddin 1988) and recent research indicates stocks from USA, Canada and southern Europe frequent the area (Dempson et al. 2010; Strøm et al. 2017; Almodóvar et al. 2020). Additionally, Japanese, and Chinese fishers exploit flying squid, *Todarodes pacificus* (Steenstrup, 1880), in oceanic regions with SST of 5–10 °C (Kidokoro et al. 2010). These conditions occur along the southern edge of the NASpG (Figure 1) in the mid-Atlantic and squid fleets using small mesh falling nets could take 1SW salmon as bycatch in this region.

The decline and collapse of Atlantic salmon stocks have been greatest in North American and southern European rivers which suggests IUU overexploitation has probably been taking place in the Labrador and Irminger sea regions of the NASpG. Exploiting salmon in this region during autumn would provide catches of 1 + SW fish (putative 2SW adults) in excellent condition after leaving the West Greenland coast (Sheehan 2019). Further work on the fine-scale delineation of Atlantic salmon ocean migration is needed to determine movements and timing of occurrence in the NASpG so that possible IUU fishing can be reliably located (Iverson et al. 2019; Park et al. 2020).

Similarly, remote regions inside and outside the EEZ areas in the far north of the Greenland, Norwegian and Barents seas that have been warming during the last 20 years now provide salmon feeding habitat in summer and autumn (Rikardsen et al. 2008; Dabrowska et al. 2020; Strøm et al. 2020). Atlantic salmon are known to occur under Arctic ice (Jensen and Lear 1980), which means they could be feeding on sympagic fauna in these regions before the ice cover melts and then on pelagic fauna when open water appears (Fortiér et al. 2006; Søreide et al. 2006; Ehrlich et al. 2020). Persistence of cyclic annual adult returns and lack of collapsed stocks to date in Norway and Russia suggests that less IUU exploitation occurs in these regions where northern European stocks predominately feed during their migration in the NASpG (Rikardsen et al. 2008; Dadswell et al. 2010; Ó Maoiléidigh et al. 2018; Strøm et al. 2018). Lack of surveillance combined with little human activity in far-north regions, however, could eventually attract more exploratory IUU fishers.

Annual reports by ICES on the status of Atlantic salmon stocks in the North Atlantic include estimates of unreported catch by member nations. During 2004 unreported catch was estimated at 1,039 *t* which dropped to 258 *t* by 2019 (ICES 2004, 2020). These data were collected by ICES from member nations, but they are unverified. Their estimates, however, do not come anywhere close to the number of missing salmon from the North Atlantic population. Also, the small legal fisheries off west Greenland (Sheehan 2017), in the St. Pierre-Miquelon EEZ (Bradbury et al. 2016a; where fishing is occurring further offshore than 20 km since France has resigned membership in NASCO) and formerly off Ireland and the UK (Bradbury et al. 2016b) cannot account for the shortfall off 1.5–2.0 million salmon a year. Unfortunately, in a recent Atlantic Salmon Trust workshop on “likely suspects" of salmon mortality at sea, participants did not list IUU fishing as a possible cause (Crozier et al. 2017).

If IUU fishing is causing the decline and impending collapse of Atlantic salmon, it would not be the first time high-seas drift fisheries have collapsed a fish population in the North Atlantic. During the period 1925–1990, a drift fishery exploited the stock of bluefin tuna in the northern North Sea and off Norway (Tiews 1978). Total landings exceeded 10,000 *t*/year before it collapsed into a flatline state after 1970 (Figure 17; ICES 2001). Vessels participating in the fishery were from Denmark, Norway, Sweden, and France. This stock, after 50 years, is just now recovering (Horton et al. 2020). Similarly, stocks of Atlantic herring off Iceland and Norway were fished to commercial extinction by drift fisheries during the 1960s (Engelhard and Heino 2004).

Discovery of the IUU fishing threat to Atlantic salmon in the North Atlantic will probably require satellite and AIS tracking (Souza et al. 2016; Kroodsma et al. 2018) unless NASCO implements ship and aircraft monitoring of the NASpG. To explain the decline of the North Atlantic salmon population since 1985, the loss of at least 3,000–5,000 *t* (1.5–2.0 million) wild adults must be accounted for annually. We suggest an undisclosed IUU fishery is the most probable cause for a shortfall of this magnitude. Essentially a IUU fishery has probably replaced the legal, high-sea fishery that existed before 1985 and was causing rapid decline of stocks across the North Atlantic which many researchers thought would collapse the North Atlantic population (Paloheimo and Elson 1974b; Scarnecchia et al. 1991; Hindar et al. 2007). Because there is apparently no recent knowledge of IUU fishing for Atlantic salmon means little; it probably just means, like other illegal activities, that it is being successfully hidden (Yablokova 1994; Telesetsky 2015; Belhabib and Le Billon 2020; Yorwood et al. 2020).

Discussion

Common features of the decline and collapse of the Atlantic salmon stocks across the North Atlantic (timing, magnitude of decline and failure to recover during the last 35 years) suggests that they are linked. Numerous researchers have carefully compared the coherence in time trends for changes in salmon life history traits and abundance during the same period and corroborate this linkage (Lehnert et al. 2019; Olmos et al. 2019, 2020). We contend that the main driver of the decline and impending collapse of the North Atlantic salmon population is probably IUU overexploitation.

Recent hypotheses for the decline of the salmon population in the North Atlantic include global climate change, the development of large-scale aquaculture, the impact of predators, a loss of marine prey, and competition with other planktivorous fishes. We will examine the potential impact of these recently proposed sources of salmon mortality in the North Atlantic and provide arguments why they are unlikely to be primarily responsible for the widespread and continuing 35-year decline in adult return abundance and collapse of Atlantic salmon stocks.

Numerous researchers have proposed that the environmental impact of global climate change on the

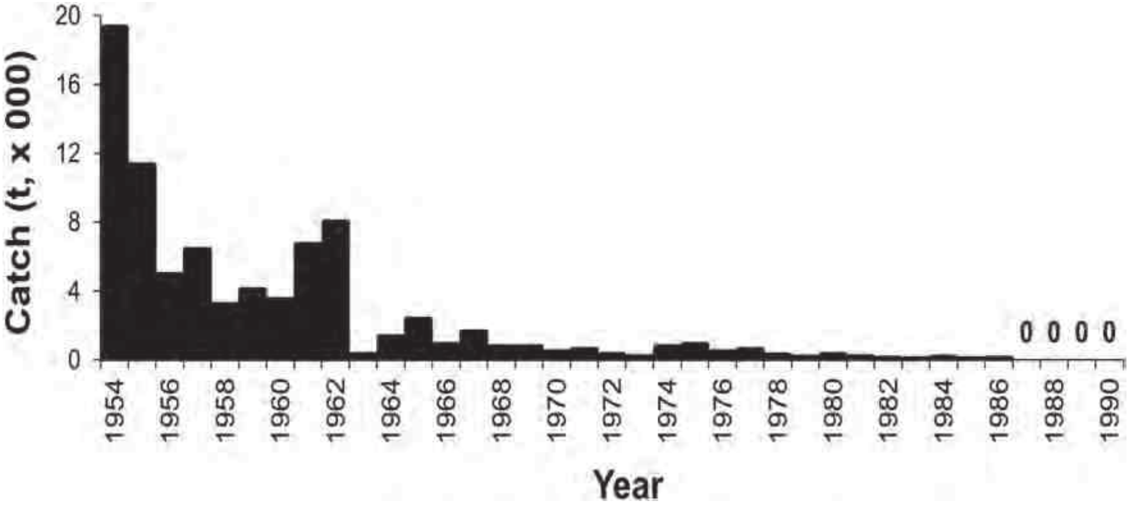

Figure 17. Reported catch (t) of bluefin tuna from the northern North Sea and off Norway during 1954–1990. Note the flatline of catches after 1962 as the stock collapsed (data from ICES 2001).

North Atlantic is the main agency in the decline of Atlantic salmon stocks (Boylan and Adams 2006; Friedland et al. 2009, 2014; Trueman et al. 2012; Mills et al. 2013; Almodóvar et al. 2019; Lehnert et al. 2019). Others propose that climate change in combination with prey and predators (Wells et al. 2008), parasites and predators (Miller et al. 2014; Vollset et al. 2016), trophic effects (Renkawitz et al. 2015) or natal freshwater environment (Nicola et al. 2018; Almodóvar et al. 2019) are causing the decline. Most contend that fluctuations in the North Atlantic Oscillation Index (NAOI), the Atlantic Multidecadal Oscillation Index (AMOI), or the rise in ocean SST has affected life history characteristics and survival of *S. salar* resulting in less fit individuals that are selected against causing the subsequent decline of stocks.

We take issue with the changing climate hypothesis driving the decline of Atlantic salmon. Our major objection is that the 35-year time frame for the decline of returning adults to home rivers no longer or poorly correlates with either the NAOI or AMOI climate cycles and many of the models are outdated (Walters and Collie 1988; Chavik 2012). When NAOI or AMOI cycling occurred in the past (pre-1985) they appeared to have had little or no effect on salmon survival and productivity, and never caused the collapse of a stock. Additionally, when researchers have compared Atlantic salmon biological characteristics among stocks, they have often found that SST variation correlated better with changes in stock attributes than either NAOI or AMOI cycling (Jensen et al. 2011; Lehnert et al. 2019; Olmos et al. 2020). When the "Great Salinity Anomaly" occurred in the NASpG during 1968–1982, which researchers maintained represented one of the most persistent and extreme variations in global climate yet in this century (Dickson et al. 1988), there was little effect on the adult abundance of the North Atlantic salmon population.

Climate cycling may be partially or wholly responsible for the natural fluctuation in cyclic abundance of adult returns (Huntsman 1931a; Antonsson et al. 1996), but is probably not responsible for the extended decline, loss of annual cycling, and collapse of stocks that is now apparent. Recent evidence from stable isotope research indicates ocean warming cannot explain synchronous declines in North American 1SW and 2SW populations (Soto et al. 2018). Further, stable isotope analysis of numerous stocks from North America and Europe provided little evidence of substantive changes in the trophic ecology of salmon migrating in the NASpG during the period 1970–2005 (Sinnatamby et al. 2009). We agree that changes in the productivity of some salmon stocks at the southern extent of the range is possibly related to the impact of climate warming on the freshwater portion of the life history (Clews et al. 2010; Russell et al. 2012; Almodóvar et al. 2019; Lehnert et al. 2019), but we argue it is probably not responsible for the extended decline of the pan-Atlantic population, especially among stocks at the mid- and northern latitudes of the freshwater range.

Atlantic salmon is an epipelagic fish and like other pelagic organisms in the NASpG can change its ocean distribution rapidly in response to annual and decadal variations in ocean temperatures (Jákupsstovu 2002; Hátún et al. 2009; Hattab et al. 2014). We argue that ocean warming probably has little effect on the survival and productivity of salmon during the oceanic stage of the life cycle. Recent research using temperature recording tags indicates salmon utilize temperatures from 1.6 to 8.4 °C during ocean migration and that their distribution and migration routes are flexible and can vary with annual changes in SST distribution (Chittenden et al. 2013; Strøm et al. 2020). In short, as the North Atlantic warms, biogeographical distribution of salmon in the NASpG, like other organisms will shift northward (Greene et al. 2008; Frainer et al. 2017; Campana et al. 2020), but it is unlikely that the area of preferred habitat will decrease causing a decline in overall feeding habitat availability and population decline. Indeed, the area of the optimum temperature zone of 4–8 °C for *S. salar* (Reddin and Shearer 1987) may be expanding (Friedland, et al. 2011). Like birds (Tingley et al. 2009), salmon probably track their Grinnellian niche through time (Soberón 2019). Even with overall warming of the North Atlantic caused by recent climate change (Friedland et al. 2014), the area of the NASpG has remained relatively stable (Hátún et al. 2009), and available at-sea habitat for marine growth of salmon although fluctuating from year to year remains relatively unchanged (Friedland and Todd 2012; Nielsen et al. 2013; Strøm et al. 2020).

The effect of changing climate has even less credence as a driver of ocean mortality when the survival of Atlantic salmon is compared to climate fluctuation over the last million years (Imbrie et al. 1993; Greene et al. 2008). Atlantic salmon obviously accommodated its fresh water and marine distributions in response to the major climate fluctuations during the Quaternary or otherwise it might now be extinct. Its entire present freshwater range in North American and a large portion of its freshwater range in Europe was covered with ice during the last glacial advance (Benn and Evans

1998; Verspoor et al. 2002; Finnegan et al. 2013). Furthermore, there has been a series of more extreme warming periods in the northern hemisphere since the last retreat of the continental glaciers than has yet occurred during the present warming trend (Alley 2000). During the Minoan and Roman warming events, 4,500 and 2,000 BP, respectively; average world temperature was 2.5 °C and 2.0 °C above present, and the writings of Julius Caesar (55 BC) inform us salmon was abundant during the latter period among populations from Gaul (France) near the present-day southern limit of its freshwater range in Europe. If present climate warming continues, stocks at the southernmost extent of the Atlantic salmon range on both continents will likely go extinct because of unsuitable freshwater habitat (Huntsman 1942; Nislow et al. 2004; Nicola et al. 2018) but those stocks will probably be replaced by colonization of northern watersheds in places like Labrador, Hudson Bay, the Canadian Arctic, Greenland, Novaya Zemlya and perhaps Spitsbergen (Nielsen et al. 2013; Jensen et al. 2014; Bilous and Dunmall 2020). It would not be the first time Atlantic salmon have recolonized northern watersheds because of climate change (Makhrov et al. 2005; Säisä et al. 2005).

An additional problem with the climate change hypothesis is that research findings often contradicted each other concerning the effect changing ocean conditions may have on the growth, condition, and survival of Atlantic salmon, and its relation to fitness of the North Atlantic population. Warming of the surface waters of the North Atlantic has been linked to poor condition of returning adults to Scottish and Norwegian rivers (Bacon et al. 2009; Hanson et al. 2013; Jonsson et al. 2016), but, in another study, data indicated that body weights of returning adults in the Northwest Atlantic had increased during recent decades and the change was correlated with thermal conditions of the winter-spring habitat (Friedland and Todd 2012). Which is correct? Could loss of size and condition of adults from the Northeast Atlantic perhaps be related to other factors such as a decline in available fish prey caused by the intense small-mesh pelagic trawl fishery for blue whiting that occurs from off Ireland and into the Norwegian Sea along the axis of the NASpG (Sandal 2006; Hátún et al. 2009; Payne et al. 2012). All the pelagic fishes captured by this fishery are a major component of the salmon diet in the North Atlantic (Lear 1972; Hansen and Pethon 1985; Jacobsen and Hansen 2000, 2001) and their overexploitation would cause repercussions to the food chain (Sandal 2006). A recent decline in size of 1SW salmon returning to European rivers since 2005 could well be one result (Bacon et al. 2009; Jonsson et al. 2016; Tom McDermott, Marine Institute, personal observation). Similarly, changing climate has been related to changes in ocean productivity and the survival and abundance of salmon stocks (Scarnecchia 1984; Turrell and Shelton 1993; Beaugrand and Reid 2012; Trueman et al. 2012). But both productivity and survival could also be related to a decline of prey availability caused by fishing up the food chain (Hjermann et al. 2004; Sandal 2006; Obradovich et al. 2014) and/or by directed IUU fishing (i.e., from gill net selectivity; Ricker 1975).

Aquaculture of Atlantic salmon has become a major industry around the North Atlantic. Farms are now established in Canada, USA, Iceland, Ireland, UK (Scotland, Shetlands, and Orkneys), Faroes, Norway, Sweden, and Spain (ICES 2020). Production of farmed salmon reached 1.75 million *t* in 2019 of which Norway and Scotland produced 78% and 11% of the total, respectively. Farmed salmon frequently escape and interact with wild salmon (Carr et al. 1997; Skilbrei et al. 2015; Forseth et al. 2017; Keyser et al. 2018). During 2002–2006 escape of farmed salmon from Scottish farms averaged 215,903 annually (Thorstad et al. 2008), and in 2019 an estimated 271,000 escaped from Norwegian farms (ICES 2020). The proportion of escaped, farmed salmon in Norwegian rivers, although as high as 30% a year during the past (Forseth et al. 2017; Diserud et al. 2019), over the last decade varied from 3 to 7% (ICES 2020). Farm escapes as large as 20,000 mature, adult fish in one event have been well documented in the northwest Atlantic (Wringe et al. 2018).

Escaped, farm salmon have been found to interact detrimentally with wild stocks in numerous ways. The escape of aquaculture juveniles from freshwater hatcheries has been shown to displace wild parr in streams (Gausen and Moen 1991; Stokesbury et al. 2001). Reproductive crossing of wild and farmed fish during spawning is known to cause genetic introgression which leads to decreased fitness of offspring for freshwater and perhaps marine survival (McGinnity et al. 2003; Karlsson et al. 2016; Keyser et al. 2018). The transmission of furunculosis to wild Norwegian populations was caused by the transfer of stocks from salmon farms in Scotland and Denmark to Norway (Johansen et al. 2011), and it was demonstrated that transmission of orthoreovirus (PRV) from farmed to wild fish has occurred in Norway but there was no resulting disease (Garseth et al. 2013). Additionally, salmon lice infestations of farmed salmon will transfer to migrating wild post-smolts and lice mortality is a major problem in some regions of the North Atlantic (Butler and Watt 2003; Bøhn et al. 2020).

Overall, however, no study has demonstrated a catastrophic effect of salmonid farming on wild Atlantic salmon that would lead to the decline and potential collapse of stocks across the North Atlantic. Hatcheries for juveniles are generally clustered close to regions where there is a high density of farms resulting in impacts on freshwater parr populations that are localized (Stokesbury et al. 2001; Carr and Whoriskey 2006). Genetic introgression of farm and wild salmon has occurred for a long period and to date study results found inconclusive results among studied populations (Karlsson et al. 2016; Verspoor et al. 2016). In Norway, where there has been 50 years of interaction between farm and wild salmon (Glover et al. 2017), and where a study found 51 of 109 stocks examined had significant genetic introgression (Johansen et al. 2011), introgression was thought to be a factor in the extirpation of perhaps only 20 out of more than 400 salmon stocks (Forseth et al. 2017). There were disease outbreaks in 38% of the more than 600+ salmon farms in Norway and escaped fish with alphavirus and PRV have ascended rivers nearby but to date there is no documentation of large impacts through infections of wild fish (Forseth et al. 2017). Infestations of migrating wild, post-smolts by salmon lice are known to be a factor in reduced returns of adults to some stocks, but poor returns have only been observed in regions where post-smolts must negotiate among intricate waterways and past multiple salmonid farms such as around the Hebrides off the west coast of Scotland (Butler and Watt. 2003), and in the long, complex fjords of western Norway (Bøhn et al. 2020; Greaker et al. 2020). In regions where post-smolts can quickly move to sea infestation has been absent or negligible (Carr and Whoriskey 2004; Lacroix and Knox 2005; Jackson et al. 2011, 2013).

Salmon lice are a natural part of the ecology of Atlantic salmon while at sea. Templeman (1968) reported that adult fish caught in the Labrador Sea had a 70–78% infection rate and that those caught off West Greenland, a 93% rate. In all cases intensity of infestation, however, was low (4–10 lice a fish). Norway has over 400 salmon stocks and 600+ salmonid farms stretching the entire length of the country (Forseth et al. 2017), and although there has been an approximate decline of 50% in adult returns since 1985 Norway is among the few countries with the least decline in adult return abundance (Otero et al. 2011; Forseth et al. 2017; Anon 2019a). In the case of numerous large stocks which are declining or have collapsed, such as the Saint John and Miramichi rivers in North America and the River Foyle in Ireland, their estuaries are distant from the nearest salmonid farm and salmon lice infestation of post-smolts has been shown to be minimal (Lacroix and Knox 2005; Jackson et al. 2013).

Escaped, farmed salmon mix with wild fish in rivers, inshore close to salmonid farms, and offshore in the NASpG. In general, post-smolts that escape or were released experimentally during spring and early summer moved rapidly seaward (Skilbrei et al. 2015; Hamoutene et al. 2018) and mixed with wild salmon in the NASpG (Hansen et al. 1999; Hansen and Jacobsen 2003). Farmed salmon adapted well to life in the sea and no difference in condition factor or diet was found between them and wild fish (Jacobsen and Hansen 2001). Annual incidence of farmed salmon among catches in the NASpG has been as high as 40% (Hansen et al. 1999) and adult return rates to natal regions although low were similar to returns of wild fish (0.1–1.1%; Skilbrei et al. 2015). Older and larger fish that escaped or were released later in the year mostly remained inshore and close to salmonid farms (Skilbrei and Wennevik 2006; Skilbrei et al. 2015; Hamoutene et al. 2018), and then moved into spawning streams in autumn where they interbred with other farmed or wild salmon (Glover et al. 2017; Wringe et al. 2018; Diserud et al. 2019). Survival rates among these salmon were relatively low after escape or release (Skilbrei et al. 2015; Hamoutene et al. 2018).

Identified piscine predators of Atlantic salmon adults while at sea in coastal waters and the NASpG include porbeagle shark, bluefin tuna, Greenland shark, *Somniosus microcepalus* (Bloch and Schneider, 1801), swordfish, *Xiphias gladius* Linnaeus, 1758, other sharks and unidentified ectothermic fishes (Templeman 1967; Wheeler and Gardner 1974; Shearer 1992; Lacroix 2014; Strøm et al. 2019). Among all recent studies in the North Atlantic using temperature and depth sensitive pop-up tags (PSAT), where predators can be identified with some reliance, porbeagles were considered responsible for predation of 13 salmon from a total of 144 released tags (9.0%), and bluefin tuna, nine (6.2%). Swordfish was responsible for two salmon predation events. No salmon predation events by Greenland shark were identified in recent studies but specimens with salmon in their stomachs have been captured off west Greenland and in the northeast Atlantic (Templeman 1967; Wheeler and Gardner 1974). Also, porbeagle has been identified as a predator in past studies with one event off Greenland (Templeman 1967) and one event in the Gulf of St. Lawrence (Joyce et al. 2002).

The occurrence of porbeagle shark predation events on salmon in the North Atlantic, however, were much lower than its sister species on salmonids in the North Pacific. Salmon shark, *Lamna ditropsis* Hubbs & Follet, 1947, are proven, as their name suggests, to be voracious predators of Pacific salmonids. Nagasawa (1998) found that the annual occurrence of salmonids in sampled salmon shark stomachs from the North Pacific varied from 39 to 68% and calculated that 12.6–25.2% of annual Pacific salmonid adult abundance was taken by this fish. Similarly, a study from the southern coast of Alaska found that 35.2% of sampled salmon shark stomachs contained salmonids (Hulbert et al. 2005), and another recent study in the same region reported that 14 of 33 (42.4%) Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum, 1792), tagged with PSAT tags were consumed by *L. ditropis* (Seitz et al. 2019). On the other hand, the impact of porbeagle on the North Atlantic salmon population appears to be limited. Whether this is the result of the current low abundance of *L. nasus* or not (Joyce et al. 2002; Skomal et al. 2021), porbeagle is clearly not a salmon shark like *L. ditropis*, nor does it probably have the effect on the Atlantic salmon population comparable to the *L. ditropis* effect on Pacific salmonids. Overall, existing research indicated that piscine predation impacts on Atlantic salmon was relatively low, and we suggest is unlikely to be a primary cause of its 35-year population decline in the North Atlantic.

There have been numerous studies of the effect of avian predators on Atlantic salmon smolts and post-smolts in estuaries and coastal regions but to our knowledge none in oceanic regions. Known avian predators include mergansers, cormorants, and gannets (Elson 1962; Baum 1997; Montevecchi et al. 2002) and it is likely other fish-eating birds such as auks or razorbills take Atlantic salmon at sea (Tucker et al. 2016). All documented avian predation impacts seldom exceeded 10% mortality of the available salmon and most authors concluded that bird predation is not a factor in the decline of *S. salar* stocks (Elson 1962; Montevecchi et al. 2002). Once upon a time, great auks, *Pinguinus impennis* Linnaeus, 1758, may have been predators of salmon on the high seas (Olson et al. 1979), but we are unlikely to know since great auks suffered anthropogenic extinction by 1852. Their former range exactly matches the present-day range of Atlantic salmon across the North Atlantic (Grieve 1885; Jordan and Storrs 1982). During the period 1984–1992, fish-eating seabird chick survival and bird populations (terns, puffins, guillemots, etc.) in the northeast and northwest Atlantic declined substantially (Gaard et al. 2002; Bacon et al. 2009; Gaston et al. 2009) concurrent with the decline in salmon abundance. Many of the North Atlantic marine bird populations have since recovered or increased (Gaard et al. 2002; Gaston et al. 2009), but the Atlantic salmon population has not.

Conversely, marine mammals are well documented as salmonid predators. Pinnipeds and cetaceans known to prey on Atlantic salmon include harbor seal, *Phoca vitulina* Linnaeus, 1758, harp seal, *Pagophilus groenlandica* Erxleben, 1777, gray seal, *Halichoerus grypus* (Fabricius, 1791), harbor porpoise, *Phocoena phocoena* (Linnaeus, 1758), bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), beluga whale, *Delphinapterus leucas* (Pallas, 1776), long-finned pilot whale, *Globicephala melas* (Traill, 1809) and killer whales, *Orcinus orca* (Linnaeus, 1758), (Shearer 1992; Middlemas et al. 2003; Vester and Hammerschmidt 2013; Strøm et al. 2018). In most studies, wild salmon predation was opportunistic and occurred in the region of estuaries, around fishing operations and other coastal sites. Studies on the food items found in pinniped and cetacean stomachs indicated salmon incidence was extremely low except around human salmon netting sites (Middlemas et al. 2003). Predation on salmon by killer whales in Norwegian fjords was directed but at a level that was considered part of normal natural mortality and not population threatening (Vester and Hammerschmidt 2013). Predation of salmon by toothed whales over continental shelfs and in the NASpG has been documented from satellite pop-up tag data but there were only five incidences out of 117 (4.2%) applied tags (Strøm et al. 2018). Likely predators were thought to be beluga (four) and pilot (one) whales. Although there has been a recent, large increase in some seal populations (Sinclair et al. 2015), this is mostly confined to inshore and shelf species such as gray seal which feed largely on benthic fishes (Middlemas et al. 2003; DFO 2011). The low-level of predation by mammals in the open ocean probably precludes their impact as a cause for the Atlantic salmon population decline in the North Atlantic.

The hypothesis that a lack of prey either from a decrease in ocean productivity or climate change has also been advanced as a factor in the pan-Atlantic decline of Atlantic salmon. Some researchers have proposed that a regime change has occurred in the North Atlantic and data suggests that plankton production in the epipelagic zone has decreased (Gaard et al. 2002; Hátún et al. 2009; Trueman et al. 2012; Almodóvar et al. 2019). A mid-water, small mesh trawl fishery for blue whiting, however, operates from off Ireland to the northern Norwegian Sea along the axis of the NASpG, the same region occupied by migrating post-smolt and adult salmon (Jákupsstovu 1988; Holm et al. 2000; Dadswell et al. 2010), and has had annual catches of 1–2 million *t* since 1998 which severely depleted the stock during 2000–2010 (Sandel 2006; Payne et al. 2012). Since the trawls are not selective, other epipelagic and mesopelagic fishes are also taken as bycatch. All these fishes are known salmon prey (Lear 1972; Jacobsen and Hansen 2000, 2001; Haugland et al. 2006; Dixon et al. 2017, 2019; Kelly et al. 2018) and their depletion would limit food resources in this region. Whether regime change or fisheries catches may be limiting food availability for Atlantic salmon in some regions remains an open question, however, salmon select a diverse suite of prey available from both the epipelagic and mesopelagic communities and can switch to whatever is available (Lear 1972; Hansen and Pethon 1985; Jákupsstovu 1988). It is unlikely the loss of some food resources is causing the steep decline of the salmon population across the North Atlantic.

Large-scale and widespread pelagic trawl fisheries occur in the northeast Atlantic for mackerel, *Scomber scombrus* Linnaeus, 1758, Atlantic herring and capelin. These fisheries operate from Norwegian coastal waters west to Greenland and from the Faroes and Iceland north to Spitsbergen (Astthorsson and Vilhjálmsson 2002; Kroodsma et al. 2018; Rybicki et al. 2020). The trawlers are known to take both post-smolt and large Atlantic salmon such as a catch of 200 1SW salmon among a catch of 800 *t* of herring off Spitsbergen (ICES 2003). On average the bycatch rate of salmon based on monitoring of the Icelandic trawler fleet has been estimated at 5.4 fish/1,000 *t* of mackerel (Olafsson et al. 2016). Although the impact of the pelagic trawl fishery on the salmon population appears to be relatively small its greatest impact may be an overall reduction of prey. Also, it was recently demonstrated that competition between post-smolts and other marine planktivorous fishes was an unlikely factor in the reduced survival of the North Atlantic salmon population (Utne et al. 2021).

Our analysis of the possible factors leading to the decline and potential collapse of the North Atlantic salmon population must conclude that previously hypothesized impacts are less likely to be the ultimate cause for this crisis. On the other hand, the potential impact of IUU fishing on Atlantic salmon, which has been implicated in the decline and collapse of many fish stocks worldwide and is threatening to drive ocean fisheries to commercial extinction (Worm et al. 2006; Costello et al. 2016; Worm 2016), should be investigated vigorously. We accept that previously proposed impacts on Atlantic salmon are contributing to the present crisis but our analysis of the altered population characteristics of North Atlantic stocks suggests that IUU overexploitation has tipped the balance leading to the potential collapse of the population.

In the past human exploitation of the Atlantic salmon population was dispersed over many stocks and legal and/or IUU exploitation would have had less effect (Hutchinson et al. 2002). Now, however, with many smaller stocks extirpated or extinct since 1985, depensatory effects are no longer functioning and the remaining large stocks are demonstrating varying degrees of overexploitation including loss of cyclic annual adult abundance, flatlines, and decreases in mean size of adults even when almost all legal North Atlantic commercial salmon fisheries are closed, and most recreational take is highly regulated. By its very definition IUU fishing cannot be reduced or closed unless fishery commissions and sovereign governments become involved and prosecute the perpetrators.

Examination of annual smolt run abundance of Atlantic salmon both in North America and Europe indicates that although there has been a large decline in adult returns, smolt abundance among many stocks remains near historic levels (DFO 2018, 2019, 2020; ICES 2020). This conundrum is perhaps best explained by the stock recruitment relationship between female spawners and filial returns. Elson (1975a) found that the Ricker stock-recruitment model projected that only 8,300 females were required to provide the necessary annual filial production for the River Foyle, Ireland even when annual adult returns could be over 100,000 fish. During the past 35 years tens of millions of wild smolts recruited annually to the North Atlantic salmon population (Breau et al. 2010; DFO 2019, 2020; ICES 2020) but annual wild adult returns have declined from an estimated 6–9 million to < 2.0 million (Friedland 1998; Friedland et al. 2014; ICES 2020). Fewer and fewer female salmon continue to support the declining population. We need to answer the question. Where have all the salmon gone?

It must be noted that the steep decline in the North Atlantic salmon population began immediately after legal, high seas fisheries in the NASpG were closed or severely restricted during 1984–1991. This fact suggests that when former high-seas fishers, who had exploited salmon off West Greenland, the Faroes or in the Norwegian Sea, observed there was no fisheries surveillance in place over the North Atlantic by 1985 they probably returned to business as usual but without any catch regulations (Mancini et al. 2011). They had the vessels, gear and knowledge that would allow them to quickly exploit the Atlantic salmon population anywhere in the NASpG whether it was with drift gill net or long-line (Jákupsstovu 1988). Also, Japanese, and Chinese squid fishers exploit the southern region of the NASpG where SST is 5–10 °C (Kidokoro et al. 2010), and possibly take 1SW salmon as by-catch, especially if they were feeding on squid attracted to their vessels at night by lights (Lear 1972; Park et al. 2020). With the development of power gear haulers, cod-end pumps, flash freezing, ultra-cold freezers, and the ability to transship to reefers or factory ships, fishers have few problems obtaining and moving IUU catches to market. If Soviet Russia could hide fleets of large factory ships and hunting vessels for whales in the world oceans for 30 years without detection (Ivashchenko and Clapham 2014), it would seem logical that other fishers can do the same in the North Atlantic.

If the decline of the wild North Atlantic salmon population is not arrested, we suggest that more stocks will continue to collapse into a flatline state and others will disappear during the coming decade. Unless decisive action is taken wild Atlantic salmon could go the way of the anadromous houting, *Coregonus oxyrinchus* (Linneaus, 1758), which is virtually extinct except for a few isolated populations (Freyhof and Schöter 2005; Borcherding et al. 2014). Even now Atlantic salmon is part of the worldwide decline of diadromous fishes (Limburg and Waldman 2009), and, because of extensive farming, could become another auroch, *Bos primigenius* Bojanus, 1827, (Ajmone-Marsan et al. 2010). The loss of so many salmon stocks will also lead to a decline in the genetic diversity of the North Atlantic population further damaging the sustainability of the species (Hendry et al. 2003). Unregulated fisheries continue to collapse fish stocks worldwide (Falsone et al. 2021), why not Atlantic salmon. North Atlantic fisheries commissions should address the situation and take the necessary steps to identify possible IUU fishing. We propose it is time to invoke the "Law of Parsimony" framed by the English Franciscan friar William of Ockham that "the simplest explanation is probably correct."

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References

Ajmone-Marsan P, Garcia JF, Lenstra JA. 2010. On the origin of cattle: how aurochs became cattle and colonized the world. Evol Anthropol. 19(4):148–157. doi:10.1002/evan.20267

Alexander DR, Galbraith P. 1982. A plan to reestablish a natural population of Atlantic salmon in the Point Wolfe River, Fundy National Park. Can Man Rep Fish Aquat Sci. 1667:8.

Alley RB. 2000. The younger Dryas cold interval as viewed from central Greenland. J. Quat. Sci. Rev. 19(1-5):213–226. doi:10.1016/S0277-3791(99)00062-1

Almodóvar A, Ayllón D, Nicola GG, Jonsson B, Elvira B. 2019. Climate driven biophysical changes in feeding and breeding environments explain the decline of southernmost European Atlantic salmon populations. Can J Fish Aquat Sci. 76(9):1581–1595. doi:10.1139/cjfas-2018-0297

Almodóvar A, Nicola GG, Ayllón D, Trueman CN, Davidson I, Kennedy R, Elvira B. 2020. Stable isotopes suggest location of marine feeding grounds of South Europe Atlantic salmon in Greenland. ICES J Mar Sci. 77(2):593–603. doi:10.1093/icesjms/fsz258

Amiro P. 2003. Population status of inner Bay of Fundy Atlantic salmon (*Salmo salar*), to 1999. Can Tech Rep Fish Aquat Sci. 2488:vi + 46.

Andrews SN, Hirtle SV, Limansaari T, Curry RA. 2019. Consumption of Atlantic salmon smolt by striped bass: a review of the predator-prey encounter literature and implications for the design of effective sampling strategies. Fishes 4(50):21. doi:10.3390/fishes4040050

Anon. 2009. A review of IUU salmon fishing and potential conservation strategies in the Russian Far East. *The Wild Salmon Center*: 21. Accessed 12/06/2020. www.wildsalmoncentre.org.

Anon. 2018. State of North American Atlantic Salmon populations. Atlantic Salmon Federation: St. Andrews, NB, Canada. Accessed 28/03/2019. www.asf.ca.

Anon. 2019a. Report of the U.S. Atlantic salmon assessment committee. U.S. Atlantic Salmon Assessment Committee Report 31-2018. Accessed 26/03/2019.

Anon. 2019b. Status of wild Atlantic salmon in Norway. In: Norw. Sci. Adv. Comm. Atl. Sal. (Forseth T, and Thorstad EB, Eds.). Accessed 24/03/2019. www.vitenskapsradet.no/Nyheter/Nyhetsartikkel/Articleld/4854.

Anon. 2020. International collaboration is a key element for success in combatting IUU fishing in the North Pacific. N Pac Anad Fish Comm Newsl. 48:3–4.

Antonsson T, Gudbergsson G, Gudjónsson S. 1996. Environmental continuity in fluctuation of fish stocks in the North Atlantic Ocean with particular reference to Atlantic salmon. N Am J Fish Manag. 16(3):540–547. doi:10.1577/1548-8675(1996)016<0540:ECIFOF > 2.3.CO;2

Aprahamian MW, Strange CD, Dimond C. 1988. Movement of Atlantic salmon, *Salmo salar* L., into the River Usk, South Wales, in relation to water quality. J Fish Biol. 33(sa):245–247. doi:10.1111/j.1095-8649.1988.tb05584.x

Arrignon J, Tane JP, Latreille M. 1988. Exploitation of the resource in France. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm. p. 29–68.

Ashley K. 2019. Wild salmon. *SPICe Briefing*. p. 19–48. Accessed 15/05/2019. www.digitalpublications.parliament.scot/ResearchBriefings/Report/2019/8/19/Wild-Salmon.

Astthorsson OS, Vilhjálmsson H. 2002. Iceland shelf LME: decadal assessment and resource sustainability. In: Sherman K, Skjoldal HR, editors. Large marine ecosystems of the North Atlantic. Amsterdam (NL): Elsevier Science. p. 219–243.

Atkins CG. 1887. The river fisheries of Maine. In: Goode GB, editor. The fisheries and fishery industries of the United States. Washington (DC): US Bureau of Fisheries, Government Printing Office. p. 673–728.

Bacon PJ, Palmer SCF, MacLean JC, Smith GW, Whyte BDM, Gurney WSC, Youngson AF. 2009. Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. ICES J Mar Sci 66(5):844–859. doi:10.1093/icesjms/fsp096

Bakke TA, Harris PD. 1998. Diseases and parasites in wild Atlantic salmon. Can J Fish Aquat Sci. 55(S1):247–266. doi:10.1139/d98-021

Baum E. 1997. Maine Atlantic salmon: a national treasure. Hermon (ME): Atlantic Salmon Unlimited. p. 224.

Beaugrand G, Reid PC. 2012. Relationships between North Atlantic salmon, [Database] plankton, and hydroclimatic change in the Northeast Atlantic. ICES J Mar Sci. 69:1559–1562.

Beland KF, Kocik JF, Van de Sande J, Sheehan TF. 2001. Striped bass predation on Atlantic salmon smolts in Maine. Northeastern Nat. 8(3):267–274. doi:10.2307/3858483

Beland P. 1996. Beluga: a farewell to whales. New York (NY): Lyons & Burford.

Belhabib D, Le Billon P. 2020. Editorial: illegal fishing is a crime. Front Mar Sci. 7:162. doi:10.3389/fmars.2020.00162

Benn DI, Evans DJA. 1998. Glaciers and glaciation. London (UK): Arnold.

Berg LS. 1935. Materials on the biology of Atlantic salmon. Izrestija Press/VRIORKH 20:3–113.

Bigelow HB, Schroeder WC. 1953. Fishes of the Gulf of Maine. Fish Bull Fish Wildl Ser. 53:577.

Bilous M, Dunmall K. 2020. Atlantic salmon in the Canadian Arctic: potential dispersal, establishment, and interaction with Arctic char. Rev Fish Biol Fisheries. 30(3):463–483. doi:10.1007/s11160-020-09610-2

Birman IB. 1979. On the similarity in the population dynamics of the Canadian salmon, *Salmo salar*, and the Amur autumn chum salmon, *Oncorhychus keta*, infraspecies autumalis. J Ich. 20:672–677.

Boerder K, Miller NA, Worm B. 2018. Global hot spots of transshipment of fish catch at sea. Sci Adv. 4(7):eaat7159. doi:10.1126/sciadv.aat7159

Bøhn T, Gjelland KØ, Serra-Llinares RM, Finstad B, Primicerio R, Nilsen R, Karlsen Ø, Sandvik AD, Skilbrei OT, Elvik KMS, et al. 2020. Timing is everything: survival of Atlantic salmon *Salmo salar* postsmolts during events of high salmon lice densities. J Appl Ecol. 57(6):1149–1160. doi:10.1111/1365-2664.13612

Borcherding J, Breukelaar AW, Winter HV, König U. 2014. Spawning migration and larval drift of anadromous North Sea houting (*Coregonus oxyrinchus*) in the River Ijssel, the Netherlands. Ecol Freshw Fish. 23(2):161–170. doi:10.1111/eff.12058

Bowlby HD, Gibson AJF. 2012. Inferring adult status and trends from juvenile density data for Atlantic salmon. N Am J Fish Manag. 32(6):1225–1236. doi:10.1080/02755947.2012.720648

Boylan P, Adams CE. 2006. The influence of broadscale climatic phenomena on long term trends in Atlantic salmon population size: an example from the River Foyle, Ireland. J Fish Biol. 68(1):276–283. doi:10.1111/j.0022-1112.2006.00893.x

Bradbury IR, Hamilton LC, Chaput G, Robertson MJ, Goraguer H, Walsh A, Morris V, Reddin D, Dempson JB, Sheehan TF, et al. 2016a. Genetic mixed stock analysis of an interceptory Atlantic salmon fishery in the Northwestern Atlantic. Fish Res. 174:234–244. doi:10.1016/j.fishres.2015.10.009

Bradbury IR, Hamilton LC, Sheehan TF, Chaput G, Robertson MJ, Dempson JB, Reddin D, Morris V, King T, Bernatchez L. 2016b. Genetic mixed stock analysis disentangles spatial and temporal variation in composition of the West Greenland Atlantic salmon fishery. ICES J Mar Sci. 73(9):2311–2321. 78:fsaa152. doi:10.1093/icesjms/fsw072

Bradbury I, Lehnert S, Messmer A, Duffy S, Verspoor E, Kess T, Gilby J, Wennevik V, Robertson M, Chaput G, et al. 2021. Range-wide genetic assignment confirms long distance oceanic migration of Atlantic salmon over half a century. ICES J Mar Sci. 78:fsaa152. doi:10.1093/icesjms/fsaa152

Breau G, Chaput G, LeBlanc P. 2010. The migration of Atlantic salmon (*Salmo salar*) smolts from the Margaree River, Nova Scotia, 2004-2009. Can Tech Rep Fish Aquat Sci. 2899:iv + 59.

Brennan RE, Rodwell LD. 2008. Sustainable management of wild Irish Atlantic salmon: keys found through the looking glass. Mar Pol. 32(6):1072–1079. doi:10.1016/j.marpol.2008.03.007

Burke WT, Freeberg M, Miles EL. 1994. United Nations resolutions on driftnet fishing: an unsustainable precedent for high seas and coastal fisheries management. Ocean Dev Int Law. 25(2):127–186. doi:10.1080/00908329409546030

Butler JRA, Middlemas SJ, McKelvey SA, McMyn I, Leyshon B, Walker I, Thompson PM, Boyd IL, Duck C, Armstrong JD, et al. 2008. The Moray Firth seal management plan: an adaptive framework for balancing the conservation of seals, salmon, fisheries, and wildlife tourism in the UK. Aquatic Conserv Mar Freshw Ecosyst. 18(6):1025–1038. doi:10.1002/aqc.923

Butler JRA, Watt J. 2003. Assessing and managing the impacts of marine salmon farms on wild Atlantic salmon in western Scotland: identifying priority rivers for conservation. In: Mills D, editor. Salmon at the edge. Oxford (UK): Blackwell Science. p. 93–118.

Caddy JF, Chandler JF. 1976. Historical statistics of landings of inshore species in the Maritime Provinces 1947-'73. Tech Rep Fish Res Bd Can. 639:239.

Campana SE, Casselman JM, Jones CM, Black G, Barker O, Evans M, Guzzo MM, Kilada R, Muir AM, Perry R. 2020. Arctic freshwater fish productivity and colonization increases with climate warming. Nat Clim Chang. 10(5):428–433. doi:10.1038/s41558-020-0744-x

Carr JW, Anderson JW, Whoriskey FG, Dilworth T. 1997. The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian River. ICES J Mar Sci. 54(6):1064–1073. doi:10.1016/S1054-3139(97)80010-0

Carr JW, Whoriskey FG. 2004. Sea lice infestation rates on wild and escaped farmed Atlantic salmon (*Salmo salar* L.) entering the Magaguadavic River, New Brunswick. Aquac Res. 35(8):723–729. doi:10.1111/j.1365-2109.2004.01094.x

Carr JW, Whoriskey FG. 2006. The escape of juvenile farmed Atlantic salmon from hatcheries into freshwater streams in New Brunswick, Canada. ICES J Mar Sci. 63(7):1263–1268. doi:10.1016/j.icesjms.2006.03.020

CEFAS. 2020. Centre for Environment, Fisheries, and Aquaculture Science. Accessed 05/06/2020. www.cefas.co.uk.

Chadwick EMP. 1985. The influence of spawning stock on production and yield of Atlantic salmon, *Salmo salar* L., in Canadian rivers. Aquacult Res. 16(1):111–119. doi:10.1111/j.1365-2109.1985.tb00300.x

Chaput G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. ICES J Mar Sci. 69(9):1538–1548. doi:10.1093/icesjms/fss013

Chaput G, Carr J, Daniels J, Tinker S, Jonsen I, Whoriskey F. 2019. Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, Northwest Atlantic. ICES J Mar Sci. 76(4):1107–1121. doi:10.1093/icesjms/fsy156

Chase S. 2003. Closing the North American mixed stock commercial fishery for wild Atlantic salmon. In: Mills D, editor. Salmon at the edge. Oxford (UK): Blackwell Science. p. 84–92.

Chavik L. 2012. The response of the circulation in the Faroe-Shetland channel to the North Atlantic Oscillation. Tellus A 64:18423.

Chick JH, Gibson-Reinemer DK, Soeken-Gittinger L, Casper AF. 2020. Invasive silver carp is empirically linked to declines of native sport fish in the upper Mississippi River system. Biol Invasions. 22(2):723–734. doi:10.1007/s10530-019-02124-4

Chittenden CM, Fauchald P, Rikardsen AH. 2013. Important open ocean areas for northern Atlantic salmon (*Salmo salar*) as estimated using a simple ambient-temperature approach. Can J Fish Aquat Sci. 70(1):101–104. doi:10.1139/cjfas-2012-0215

Christensen O, Lear WH. 1980. Distribution and abundance of Atlantic salmon at west Greenland. Rap Pro-Erb Réun Cons Intern l'Explor Mer. 176:22–35.

CIUUVL. 2020. Combined IUU Vessel List. www.iuu-vessels.org.

Clarke SC, McAllister MK, Kirkpatrick RC. 2009. Estimating legal and illegal catches of Russian Sockeye salmon from trade and market data. ICES J Mar Sci. 66(3):532–545. doi:10.1093/icesjms/fsp017

Clews E, Durance I, Vaughan IP, Ormerod SJ. 2010. Juvenile salmonid populations in a temperate river system track synoptic tends in climate. Glob Change Biol. 16(12):3271–3283. doi:10.1111/j.1365-2486.2010.02211.x

Condron A, Deconto R, Bradley RS, Juanes F. 2005. Multidecadal North Atlantic climate variability and its effect on North American Atlantic salmon abundance. Geophys Res Lett. 32:L23703.

Costello C, Ovando D, Clavelle T, Strauss CK, Hilborn R, Melnychuk MC, Branch TA, Gaines SD, Szuwalski CS, Cabral RB, et al. 2016. Global fishery prospects under contrasting management regimes. Proc Natl Acad Sci USA. 113(18):5125–5129. doi:10.1073/pnas.1520420113

Crozier WW, Kennedy GJA. 1993. Marine survival of wild and hatchery reared Atlantic salmon (*Salmo salar* L.) from the River Bush, Northern Ireland. In: Mills D, editor. Salmon in the Sea and new enhancement strategies. Oxford (UK): Fishing News Books. p. 139–162.

Crozier WW, Whelan K, Buoro M, Chaput G, Daniels J, Grant S, Hyatt K, Irvine J, Ó'Maoiléidagh N, Provost E, Riot E, et al. 2017. Atlantic salmon mortality at sea: developing an evidence based 'likely suspects' framework. Atl Sal Trust Works. Accessed 15/04/2020. www.atlanticsalmontrust.org.

Cuinat R. 1988. Atlantic salmon in an extensive French river system; the Loire-Allier. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm. p. 389–399.

Cunjak RA, Therrien J. 1998. Interstage survival of wild juvenile Atlantic salmon *Salmo salar* L. Fish Manag Ecol. 5(3):209–223. doi:10.1046/j.1365-2400.1998.00094.x

Dabrowska AM, Wiktor JM, Jr, Matgorzata M, Wiktor JM. 2020. Planktonic protists of the eastern Nordic seas and Fram Strait: spatial changes related to hydrography during early summer. Fron Mar Sci. doi:10.3389/fmars.2020-00557

Dadswell MJ. 1968. Atlantic salmon (*Salmo salar*) investigations in the Point Wolfe and Upper Salmon Rivers, Fundy National Park. Can. Wildl. Serv. Manu. Rep. Accessed 15/10/2019. www.parkscanada.gc.ca/en/pn-np/fundy.

Dadswell MJ. 2000. Where have all the salmon gone?Nova Outdoors 9:17–20.

Dadswell MJ, Bradford R, Leim AH, Melvin GD, Appy RG, Scarratt DJ. 1984. A review of fish and fisheries research in the Bay of Fundy between 1976 and 1983. In: Gordon DC, Jr, Dadswell MJ, editors. Update on marine environmental consequences of tidal power development in the upper reaches of the Bay of Fundy, Vol. 1256. Can Tech Rep Fish Aquat Sci, Ottawa. p. 163–294.

Dadswell MJ, Spares AD, Reader JM, Stokesbury MJW. 2010. The North Atlantic Subpolar Gyre and the marine migration of Atlantic salmon *Salmo salar*: the 'Merry-Go-Round' hypothesis. J Fish Biol. 77:435–467. doi:10.1111/j.1095-8649.2010.02673.x

Daniels J, Chaput G, Carr J. 2018. Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) in the Miramichi estuary using acoustic telemetry. Can J Fish Aquat Sci. 75(11):1811–1822. doi:10.1139/cjfas-2017-0373

Daniels J, Sutton S, Webber D, Carr J. 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolts (*Salmo salar*) as suggested by a novel acoustic tag. Anim Biotelem. 7:16–26.

Davidson K, Bielak AT. 1993. New enhancement strategies in action. In: Mills D, editor. Salmon in the Sea and new enhancement strategies. Oxford (UK): Fishing News Books. p. 299–320.

Dempson JB, O'Connell MF, Schwarz CJ. 2004. Spatial and temporal trends in abundance of Atlantic salmon, *Salmo salar*, in Newfoundland with emphasis on impacts of the 1992 closure of the commercial fishery. Fisheries Manage. 11(6):387–402. doi:10.1111/j.1365-2400.2004.00407.x

Dempson JB, Braithwaite VA, Doherty D, Power M. 2010. Stable isotope analysis of marine feeding signatures of Atlantic salmon in the North Atlantic. ICES J Mar Sci. 67(1):52–56. doi:10.1093/icesjms/fsp227

Dempson JB, Robertson MJ, Pennell CJ, Furey G, Bloom M, Shears M, Ollerhead LMV, Clarke KD, Hinks R, Robertson GL. 2011. Residency time, migration route and survival of Atlantic salmon *Salmo salar* smolts in a Canadian fjord. J Fish Biol. 78(7):1976–1992. doi:10.1111/j.1095-8649.2011.02971.x

DFO (Department of Fisheries and Oceans). 1999a. Stock status of Atlantic salmon (Salmo salar) in the Miramichi River, 1998. Can. Stock Ass. Sec. Res. Doc. 99/049.

DFO. 1999b. Atlantic salmon Maritime provinces overview for 1999. Sci. Stock Stat. Rep. D3-XX.

DFO. 2011. Impacts of grey seals on fish populations in eastern Canada. Canadian Science Advisory Secretariat, Science Advisory Report 2011/071.

DFO. 2013. Recovery potential assessment for southern upland salmon. Can. Sci. Adv. Secr., Sci. Adv. Rep. 2013/009.

DFO. 2014. Stock assessment of Newfoundland and Labrador-2013. Can. Sci. Adv. Secr., Sci. Adv. Rep. 2014/023.

DFO. 2017. Update of indicators of Atlantic salmon (*Salmo salar*) in DFO Gulf region salmon fishing areas 15-18 for 2016. Can. Sci. Adv. Secr., Sci. Res. 2017/013.

DFO. 2018. Stock assessment of Newfoundland and Labrador Atlantic salmon-2017. Can. Sci. Adv. Secr., Sci. Adv. Rep. 2018/034.

DFO. 2019. Update on indicators of Atlantic salmon (*Salmo salar*) in DFO Gulf region, salmon fishing areas 15-18 for 2018. Can. Sci. Adv. Secr., Sci. Res. 2019/021.

DFO. 2020. Stock status update of Atlantic salmon (*Salmo salar*) in salmon fishing areas (SFA) 19-21 and 23. Can. Sci. Adv. Secr., Sci. Res. 2020/002.

Dickson RR, Meincke J, Malmberg SA, Lee AJ. 1988. The 'Great Salinity Anomaly' in the northern North Atlantic 1968-1982. Prog Ocean. 20(2):103–151. doi:10.1016/0079-6611(88)90049-3

Dickson RR, Turrell WR. 2000. The NAO: the dominant atmospheric process effecting oceanic variability in home, middle and distant waters of European Atlantic salmon. In: Mills D, editor. The ocean life of Atlantic Salmon. Oxford (UK): Blackwell Science. p. 92–115.

Diserud OH, Fiske P, Sægrov H, Urdal K, Aronsen T, Lo H, Barlaup BT, Niemelä E, Orell P, Erkinaro J, et al. 2019. Escaped farmed Atlantic salmon in Norwegian rivers during 1982-2013. ICES J Mar Sci. 76(4):1140–1150. doi:10.1093/icesjms/fsy202

Dixon HJ, Dempson JB, Power M. 2019. Short-term temporal variation in inshore/offshore feeding and trophic niches of Atlantic salmon *Salmo salar* off West Greenland. Mar Ecol Prog Ser. 610:191–203. doi:10.3354/meps12841

Dixon HJ, Dempson JB, Sheehan TF, Renkawitz MD, Power M. 2017. Assessing the diet of North American Atlantic salmon *Salmo salar* off the Greenland coast using gut contents and sable isotope analyses. Fish Oceanogr. 26(5):555–568. doi:10.1111/fog.12216

Dumas J, Prouzet P. 2003. Variability of demographic parameters and population dynamics of Atlantic salmon (*Salmo salar* L.) in a south-west French river. ICES J Mar Sci. 60(2):356–370. doi:10.1016/S1054-3139(03)00003-1

Dunfield RW. 1985. The Atlantic salmon in the history of North America. Spec Pub Can Fish Aquat Sci. 80:181.

Ehrlich J, Schaafsma FL, Blulm BA, Peeken I, Castellani G, Brandt A, Flores H. 2020. Sympagic fauna in and under Arctic pack ice in the annual sea-ice system of the new Arctic. Fron Mar Sci. 7:452. doi:10.3389/fmars.2020.00452

Elson PF. 1962. Predator-prey relationships between fish-eating birds and Atlantic salmon. Bull Fish Res Bd Can. 133:87.

Elson PF. 1967. Effects on wild young salmon of spraying DDT over New Brunswick forests. J Fish Res Bd Can. 24(4):731–767. doi:10.1139/f67-066

Elson PF. 1975a. The impact of fisheries and environmental changes on the management of Atlantic salmon of the Foyle River system, Ireland. In: Elson PF, Tuomi ALW, editors. The Foyle fisheries: new basis for rational management. Londonderry (UK): The Foyle Fisheries Commission. p. 1–194.

Elson PF. 1975b. Atlantic salmon rivers smolt production and optimal spawning: an overview of natural production. Intern Atl Sal Found Spec Pub Ser. 6:96–119.

Elson PF, Meister AL, Saunders JW, Saunders RL, Sprague JB, Zitko V. 1973. Impact of chemical pollution on Atlantic salmon in North America. In: Smith MW, Carter WM, editors. Proc Intern Sym Atl. Sal.: Manag. Biol. Surv. Spec. Fredericton (NB): Unipress. p. 83–110.

Engelhard GH, Heino M. 2004. Maturity changes in Norwegian spring-spawning herring before, during and after a major population collapse. Fish Res. 66(2-3):299–310. doi:10.1016/S0165-7836(03)00195-4

Erkinaro J, Czorlich Y, Orell P, Kuusela J, Falkegård M, Länsman M, Pulkkinen H, Primmer CR, Niemelä E. Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river. Can J Fish Aquat Sci. 76(1):42–55. 2019. doi:10.1139/cjfas-2017-0343

Ewell C, Cullis-Suzuki S, Ediger M, Hocevar J, Miller D, Jacquet J. 2017. Potential ecological and social benefits of a moratorium on transshipment on the high seas. Mar Pol. 81:293–300. doi:10.1016/j.marpol.2017.04.004

Fairchild WL, Swansburg ER, Arsenault JT, Brown SB. 1999. Does an association between pesticide use and subsequent declines in catch of Atlantic salmon (*Salmo* salar) represent a case of endocrine disruption. Environ Health Pers. 107(5):349–367. doi:10.1289/ehp.99107349

Falsone FD, Scannella D, Geraci ML, Gancitano V, Vitale S, Fiorentino F. 2021. How to get collapse of a fishery: the case of *Lepidopus caudatus* (Pisces: Trichiuridae) in the Strait of Sicily (Central Mediterranean). Front Mar Sci. 20. doi:10.3389/fmars.2020.584601

FAO (World Food and Agriculture Organization). 2003. The extent and effects of IUU fishing in areas of competence. Accessed 16/12/2020. www.fao.org/3/y5361e/y5361e06.html.

Ferguson JW, Ploskey GR, Leonardsson K, Zabel RW, Lundqvist H. 2008. Combining turbine blade strike and life cycle models to assess mitigation strategies for fish passing dams. Can J Fish Aquat Sci. 65(8):1568–1585. doi:10.1139/F08-078

Finnegan AK, Griffiths AM, King RA, Machado-Schiaffino G, Porcher J-P, Garcia-Vazquez E, Bright D, Stevens JR. 2013. Use of multiple markers demonstrates a cryptic western refugium and postglacial colonisation routes of Atlantic salmon (*Salmo salar* L.) in Northwest Europe. Heredity. 111(1):34–43. doi:10.1038/hdy.2013.17

Flávio H, Kennedy R, Ensing D, Jepsen N, Aarestrup K. 2020. Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometers of a river monitored for stock assessment. Fish Manag Ecol. 27(1):92–101. doi:10.1111/fme.12405

Forseth T, Barlaup BT, Finstad B, Fiske P, Gjøsæter H, Falkegård M, Hindar A, Mo TA, Rikardsen AH, Thorstad EB, et al. 2017. The major threats to Atlantic salmon in Norway. ICES J Mar Sci. 74(6):1496–1513. doi:10.1093/icesjms/fsx020

Fortiér L, Sirois P, Michaud J, Barber D. 2006. Survival of Arctic cod larvae (*Boreogadus saida*) in relation to sea ice and temperature in the Northeast Water polynya (Greenland Sea). Can J Fish Aquat Sci. 63(7):1608–1616. doi:10.1139/f06-064

Frainer A, Primicerio R, Kortsch S, Aune M, Dolgov AV, Fossheim M, Aschan MM. 2017. Climate driven changes in functional biogeography of Arctic marine fish communities. Proc Natl Acad Sci USA. 114(46):12202–12207. doi:10.1073/pnas.1706080114

Francis RICC, Clark MR. 1998. Inferring spawning migrations of orange roughy (*Hoplostethus atlanticus*) from spawning ogives. Mar Freshwater Res. 49(2):103–108. doi:10.1071/MF97253

Freyhof J, Schöter C. 2005. The houting (*Coregonus oxyrinchus* L.) (Salmoniformes: Coregonidae), a globally extinct species from the North Sea basin. J Fish Biol. 67(3):713–729. doi:10.1111/j.0022-1112.2005.00771.x

Friedland KD. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. Can J Fish Aquat Sci. 55(S1):119–130. doi:10.1139/d98-003

Friedland KD. 2002. Emerging science and management issues with Atlantic salmon. In: Lynch KD, Jones ML, Taylor WW, editors. Sustaining North American Salmon: perspectives across regions and disciplines. Bethesda (MD): American Fisheries Society. p. 117–136.

Friedland KD, Dutil J-D, Sadusky T. 1999. Growth patterns in postsmolts and the nature of the marine juvenile nursery for Atlantic salmon, *Salmo salar*. Fish Bull. 97:472–481.

Friedland KD, Hansen LP, Dunkley DA, Maclean JC. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. ICES J Mar Sci. 57(2):419–429. doi:10.1006/jmsc.1999.0639

Friedland KD, Hass RE, Sheehan TF. 1996. Post-smolt growth, maturation and survival of two stocks of Atlantic salmon. Fish Bull. 94:654–663.

Friedland KD, MacLean JC, Hansen LP, Peyronnet AJ, Karlsson L, Reddin DG, Ó Maoiléidigh N, McCarthy JL. 2009. The recruitment of Atlantic salmon in Europe. ICES J Mar Sci. 66(2):289–304. doi:10.1093/icesjms/fsn210

Friedland KD, Manning JP, Link JS, Gilbert JR, Gilbert AT, O'Connell AF, Jr. 2012. Variation in wind and piscivorous predator fields affecting the survival of Atlantic salmon (*Salmo salar*) in the Gulf of Maine. Fish Manag Ecol. 19(1):22–35. doi:10.1111/j.1365-2400.2011.00814.x

Friedland KD, Shank BV, Todd CD, McGinnity P, Nye A. 2014. Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation. J Mar Sys. 133:77–87. doi:10.1016/j.jmarsys.2013.03.003

Friedland KD, Todd CD. 2012. Changes in northwest Atlantic arctic and subarctic conditions and the growth response of Atlantic salmon. Polar Biol. 353(4):593–602. doi:10.1007/s00300-011-1105-z

Funge-Smith S, Lee R, Leete M. 2015. Regional review of illegal, unreported and unregulated (IUU) fishing by foreign vessels. Asia-Pacific Fish, Pac. Fish. Comm. RAP Pub 2015/09.

Gaard E, Hansen B, Olsen B, Reinert J. 2002. Ecological features and trends in the physical environment, plankton, fish stocks, and seabirds in the Faroe shelf ecosystem. In: Sherman K, Skjoldal HR, editors. Large marine ecosystems of the North Atlantic. Amsterdam (NL): Elsevier Science. p. 245–265.

Garseth ÅH, Ekrem T, Biering E. 2013. Phylogenetic evidence of long-distance dispersal and transmission of piscine reovirus (PRV) between farmed and wild Atlantic salmon. PLoS One. 8(12):e82202. doi:10.1371/journal.pone.0082202

Gaston AJ, Bertram DF, Boyne AW, Chardine JW, Davoren G, Diamond AW, Hedd A, Montevecchi WA, Hipfner JM, Lemon MJF, Mallory ML, et al. 2009. Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. Environ Rev. 17:267–286. doi:10.1139/A09-013

Gausen D, Moen V. 1991. Large scale escapes of Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. Can J Fish Aquat Sci. 48(3):426–438. doi:10.1139/f91-055

Gee AS, Milner NJ. 1980. Analysis of 70-year catch statistics for Atlantic salmon (*Salmo salar*). J Appl Ecol. 17(1):41–57. doi:10.2307/2402962

George AF. 1982. Cyclic variations in the return migration of Scottish salmon by sea- age, c. 1790-1976. Master of Science, Open University, Scotland. doi:10.21954/ou.ro.0000f7df

Gibson AJF, Amiro P, Robichaud-LeBlanc KA. 2003. Densities of juvenile Atlantic salmon (Salmo salar) in inner Bay of Fundy rivers during 2000 and 2002 with reference to past abundance inferred from catch statistics and electrofishing surveys. Can. Sci. Adv. Secr. Res. Doc. 2003/121.

Gibson AJF, Halfyard EA, Bradford RG, Stokesbury MJW, Redden AM. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. Can J Fish Aquat Sci. 72(5):728–741. doi:10.1139/cjfas-2014-0245

Gibson RJ, Myers RA. 1986. A comparative review of juvenile Atlantic salmon production in North America and Europe. In: Crozier WW, Johnston PM, editors. Proc. 17th Ann. Study Course. Inst. Fish. Mange. University of Ulster at Coleraine, Northern Ireland. p. 14–48.

Gilbey J, Wennevik V, Bradbury IR, Fiske P, Hansen LP, Jacobsen JA, Potter T. 2017. Genetic stock identification of Atlantic salmon caught in the Faroese fishery. Fish Res. 187:110–119. doi:10.1016/j.fishres.2016.11.020

Glover KA, Solberg MF, McGinnity P, Hindar K, Verspoor E, Coulson MW, Hansen MM, Araki H, Skaala Ø, Svåsand T. 2017. Half a century of interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. Fish Fish. 18(5):890–927. doi:10.1111/faf.12214

Greaker M, Vormedal I, Rosendal K. 2020. Environmental policy and innovation in Norwegian fish farming: resolving the sea lice problem. Mar Pol. 117:103942. doi:10.1016/j.marpol.2020.103942

Greene CH, Pershing AJ, Cronin TM, Ceci N. 2008. Arctic climatechange and its impacts on the ecology of the North Atlantic. Ecology 89(11 Suppl):S24–S38. doi:10.1890/07-0550.1

Gregory SD, Ibbotson AT, Riley WD, Nevoux M, Lauridsen RB, Russell IC, Britton JR, Gillingham PK, Simmons OM, Rivot E. 2019. Atlantic salmon return rate increases with smolt length. ICES J Mar Sci. 76(6):1702–1712. doi:10.1093/icesjms/fsz066

Grieve S. 1885. The Great Auk, or Garefowl: its history, archaeology and remains. London (UK): C. Thomas.

Guðjónsson S, Einarsson SM, Jónsson IR, Guðbrandsson J. 2015. Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. Can J Fish Aquat Sci. 72(7):1087–1098. doi:10.1139/cjfas-2014-0562

Halfyard EH. 2014. The stuarine and arly arine urvival of Atlantic almon: estimation, orrelates, and cological ignificance. Doctor of Philosophy, Dalhousie University, NS, Canada. Accessed 10/06/2020. www.dalspace.library.dal.ca.

Hamoutene D, Cote D, Marshall K, Donnet S, Cross S, Hamilton LC, McDonald S, Clarke KD, Pennell C. 2018. Spatial and temporal distribution of farmed Atlantic salmon after experimental releases from sea cages in Newfoundland (Canada). Aquaculture 492:147–156. doi:10.1016/j.aquaculture.2018.03.040

Hansen LP, Jacobsen JA. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the oceanic areas north of the Faroes Islands. ICES J Mar Sci. 60(1):110–119. doi:10.1006/jmsc.2002.1324

Hansen LP, Jacobsen JA, Lund RA. 1999. The incidence of escaped farmed Atlantic salmon (*Salmo salar* L.) in the Faroese fishery and estimates of catches of wild salmon. ICES J Mar Sci. 56(2):200–206. doi:10.1006/jmsc.1998.0437

Hansen LP, Pethon P. 1985. The food of Atlantic salmon, *Salmo salar* L., caught by long-line in northern Norway waters. J Fish Biol. 26(5):553–562. doi:10.1111/j.1095-8649.1985.tb04296.x

Hanson NN, Wurster CM, Eimf C, Todd CD. 2013. Reconstructing marine life- history strategies of wild Atlantic salmon from stable isotope composition of adults. Mar Ecol Prog Ser. 475:249–266. doi:10.3354/meps10066

Hartgers EM, Buijse AD. 2002. The role of Lake Ijsselmeer, a closed off estuary of the River Rhine in rehabilitation of salmonid populations. Fish Manag Ecol. 9(3):127–138. doi:10.1046/j.1365-2400.2002.00283.x

Hattab T, Albouy C, Lasram FBR, Somot S, Le Loc'h F, Leprieur F. 2014. Towards a better understanding of climate change on marine species distribution: a multiscale modelling approach. Glob Ecol Biog. 23(12):1417–1429. doi:10.1111/geb.12217

Hátún H, Payne MR, Beaugrand G, Reid PC, Sandø AB, Drange H, Hansen B, Jacobsen JA, Bloch D. 2009. Large biogeographical shifts in the northeastern Atlantic Oscillation: from the subpolar gyre to blue whiting and pilot whales. Prog Ocean. 80(3-4):149–162. doi:10.1016/j.pocean.2009.03.001

Haugland M, Holst JC, Holm M, Hansen LP. 2006. Feeding of Atlantic salmon (*Salmo salar*) post-smolts in the northeast Atlantic. ICES J Mar Sci. 63(8):1488–1500. doi:10.1016/j.icesjms.2006.06.004

Havn TB, Thorstad EB, Teichert MAK, Saether SA, Heermann L, Hedger RD, Tambets M, Diserud OH, Borcherding J, Økland F. 2018. Hydro power-related mortality and behaviour of Atlantic salmon smolts in the River Sieg, a German tributary to the Rhine. Hydrobiologia. 805(1):273–290. doi:10.1007/s10750-017-3311-3

Hendry AP, Letcher BH, Gries G. 2003. Estimating natural selection acting on stream-dwelling Atlantic salmon: implications for the restoration of extirpated populations. Conserv Biol. 17(3):795–805. doi:10.1046/j.1523-1739.2003.02075.x

Hesthagen T, Hansen LP. 1991. Estimates of the annual losses of Atlantic salmon *Salmo salar* L. in Norway due to acidification. Aquacult Res. 22(1):85–92. doi:10.1111/j.1365-2109.1991.tb00497.x

Hesthagen T, Larsen BM, Fiske P. Liming restores Atlantic salmon (*Salmo salar*) populations in acidified Norwegian rivers. Can J Fish Aquat Sci. 68(2):224–231. 2011. doi:10.1139/F10-133

Hindar K, Leaniz CG, Koljonen M-L, Tufjo J, Youngson AF. 2007. Fisheries exploitation. In: Verspoor E, Stradmeyer L, Nielsen J, editors. The Atlantic Salmon: genetics, conservation, and management. Oxford (UK): Blackwell Publishing. p. 306–331.

Hislop JRG, Shelton RGJ. 1993. Marine predators and prey of Atlantic salmon (*Salmo salar* L.). In: Mills D, editor. Salmon in the Sea and new enhancement strategies. Oxford (UK): Fishing News Books. p. 139–162.

Hjermann DØ, Ottersen G, Stenseth NC. 2004. Competition among fishermen and fish causes the collapse of Barents Sea capelin. Proc Natl Acad Sci USA. 101(32):11679–11684. doi:10.1073/pnas.0402904101

Holbrook CM, Kinnison MT, Zydlewski J. 2011. Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine: a pre-restoration assessment. Trans Am Fish Soc. 140(5):1255–1268. doi:10.1080/00028487.2011.618356

Holm M, Holst JC, Hansen LP. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. ICES J Mar Sci. 57(4):955–964. doi:10.1006/jmsc.2000.0700

Horodysky AZ, Cooke SJ, Graves JE, Brill RW. 2016. Fisheries conservation on the high seas: linking conservation physiology and fisheries ecology for management of large pelagic fishes. Conserv Physiol. 4(1):cov059. doi:10.1093/conphys/cov059

Horton TW, Block BA, Drumm A, Hawkes LA, O'Cuaig M, Maoiléidigh NÓ, O'Neill R, Schallert RJ, Stokesbury MJW, Witt MJ. 2020. Tracking Atlantic bluefin tuna from foraging grounds off the west coast of Ireland. ICES J Mar Sci. 77(6):2066–2077. doi:10.1093/icesjms/fsaa090

Houde EP. 2016. Recruitment variability. In: Jakobsen T, Fogarty MJ, Megrey BA, Moksness E, editors. Fish reproductive biology: implications for assessment and management. New York (NY): John Wiley & Sons. p. 98–187.

Hulbert LB, Aires-da-Silva AM, Gallucci VF, Rice JS. 2005. Seasonal foraging movements and migratory patterns of female *Lamna ditropis* tagged in Prince William Sound, Alaska. J Fish Biol. 67(2):490–509. doi:10.1111/j.0022-1112.2005.00757.x

Huntsman AG. 1931a. Periodic scarcity of salmon. Fish Res Bd Can Atl Prog Rep. 2:16–17.

Huntsman AG. 1931b. The maritime salmon of Canada. Bull Biol Bd Can. 21:99.

Huntsman AG. 1941. Cyclical abundance and birds versus salmon. J Fish Res Bd Can. 5b(3):227–235. doi:10.1139/f40-024

Huntsman AG. 1942. Death of salmon and trout with high temperature. J Fish Res Bd Can. 5c(5):485–501. doi:10.1139/f40-051

Huntsman AG. 1958. Shubenacadie salmon. J Fish Res Bd Can. 15(6):1213–1218. doi:10.1139/f58-064

Hutchings JA. 1996. Spatial and temporal variation in the density of Northern Cod and a review of hypotheses for the stock's collapse. Can J Fish Aquat Sci. 53:943–962.

Hutchings JA. 2000. Collapse and recovery of marine fishes. Nature 406(6798):882–885. doi:10.1038/35022565

Hutchings JA, Jones MEB. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Can J Fish Aquat Sci. 55(S1):22–47. doi:10.1139/d98-004

Hutchinson P, Welch D, Boehlert G, Whelan K. 2002. Causes of marine mortality of salmon in the North Pacific and North Atlantic Oceans and in the Baltic Sea. N Pac Andro Fish Comm Tech Rep. 4:93–96.

Hvidsten NA, Møkkelgjerd PI. 1987. Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna. J Fish Biol. 30(3):273–280. doi:10.1111/j.1095-8649.1987.tb05752.x

ICES. 2001. Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak (WGNSSK). ICES CM 2001/ACFM:07.

ICES. 2003. Report of the ICES advisory committee on fisheries management 2003. ICES Coop. Res. Rep. 248.

ICES. 2015. Working group on North Atlantic salmon (WGNAS). ICES CM 2015/ACOM:09.

ICES. 2019. Working group on North Atlantic salmon (WGNAS). ICES Sci. Rep. 1(16).

ICES. 2020. Working group on North Atlantic salmon (WGNAS). ICES Sci. Rep. 2(21).

Imbrie J, Berger A, Boyle EA, Clemens SC, Duffy A, Howard WR, Kukla G, Kutzbach J, Martinson DG, McIntyre A, et al. 1993. On the structure and origin of major glaciation cycles. 2. The 100,000-year cycle. Paleocean Paleoclim. 8(6):699–735. doi:10.1029/93PA02751

Ivashchenko YV, Clapham PJ. 2014. Too much is never enough: the cautionary tale of Soviet whaling. Mar Fish Rev. 76(1-2):1–21. doi:10.7755/MFR.76.1_2.1

Iverson SJ, Fisk AT, Hinch SG, Flemming JM, Cooke SJ, Whoriskey FG. 2019. The Ocean Tracking Network: advancing frontiers in aquatic science and management. Can J Fish Aquat Sci. 76(7):1041–1051. doi:10.1139/cjfas-2018-0481

Jackson D, Cotter D, ÓMaoiléidigh N, O'Donohoe P, White J, Kane F, Kelly S, McDermott T, McEvoy S, Drumm A, et al. 2011. Impact of early infestation with salmon louse *Lepeophtheirus salmonis* on the subsequent survival of outwardly migrating Atlantic salmon smolt from a number of rivers on Ireland's south and west coasts. Aquaculture 319(1-2):37–40. doi:10.1016/j.aquaculture.2011.06.042

Jackson D, Cotter D, Newell J, McEvoy S, O'Donohoe P, Kane F, McDermott T, Kelly S, Drumm A. 2013. Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. J Fish Dis. 36(3):273–281. doi:10.1111/jfd.12054

Jacobsen JA, Hansen LP. 2000. Feeding habits of Atlantic salmon at different live stages at sea. In: Mills D, editor. The Ocean Life of Atlantic Salmon: environmental and biological factors influencing survival. Oxford (UK): Blackwell Science. p. 170–192.

Jacobsen J, Hansen LP. 2001. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the northeast Atlantic. ICES J Mar Sci. 58(4):916–933. doi:10.1006/jmsc.2001.1084

Jákupsstovu SH. 1988. Exploitation and migration of salmon in Faroese waters. In: Mills D, editor. Atlantic salmon: planning for the future. London (UK): Croom Helm. p. 458–482.

Jákupsstovu SHI. 2002. The pelagic fish stocks, pilot whales and squid in Faroese waters-migration pattern, availability to fisheries and possible links to oceanographic events. ICES CM 2002/N:07.

Jensen AJ, Fiske P, Hansen LP, Johnsen BO, Mork KA, Næsje TF. 2011. Synchrony in marine growth among Atlantic salmon (*Salmo salar*) populations. Can J Fish Aquat Sci. 68(3):444–457. doi:10.1139/F10-156

Jensen AJ, Karlsson S, Fiske P, Hansen LP, Østborg GM, Hindar K. 2014. Origin and life history of Atlantic salmon (*Salmo salar*) near their northern most oceanic limit. Can J Fish Aquat Sci. 71(11):1740–1746. doi:10.1139/cjfas-2014-0169

Jensen AJ, Zubchenko AV, Heggberget IG, Hvisssten NA, Johnson BO, Kuzmin O, Loenko AA, Lund RV, Martynov VG, Naeje, TF, et al. 1999. Cessation of the Norwegian drift net fishery: changes observed in Norwegian and Russian populations of Atlantic salmon. ICES J Mar Sci. 56(1):84–95. doi:10.1006/jmsc.1998.0419

Jensen JM. 1967. Atlantic salmon caught in the Irminger Sea. J Fish Res Bd Can. 24(12):2639–2640. doi:10.1139/f67-215

Jensen JM. 1980. Recaptures of salmon at west Greenland tagged as smolts outside Greenland waters. Rap Proces-Erb Reun Cons Intern L'Explor Mer. 176: 114–121.

Jensen JM. 1988. Exploitation and migration of salmon on the high seas in relation to Greenland. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm. p. 438–457.

Jensen JM, Lear WH. 1980. Atlantic salmon caught in the Irminger Sea and at East Greenland. J Northw Atl Fish Sci. 1:55–64. doi:10.2960/J.v1.a6

Jessop BM. 1975. Investigation of the salmon (Salmo salar) smolt migration of the Big Salmon River, New Brunswick, 1966-72. Fish. Mar. Ser., Dep. Envir. Tech. Rep. MAR/T-75-1.

Johansen L-H, Jensen I, Mikkelsen H, Bjørn P-A, Jansen PA, Bergh Ø. 2011. Disease interaction and pathogen exchange between wild and farmed fish populations with special reference to Norway. Aquaculture 315(3-4):167–186. doi:10.1016/j.aquaculture.2011.02.014

Johnson BO, Jensen AJ. 1991. The *Gyrodactylus* story in Norway. Aquaculture 98:289–302.

Jones RA. 1988. Atlantic salmon restoration in the Connecticut River. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm. p. 415–426.

Jones RA, Anderson L, Clarke CN. 2014. Assessment of the recovery potential for the outer Bay of Fundy population of Atlantic salmon (*Salmo salar*): status, trends, distribution, life history characteristics and recovery targets. Can. Sci. Adv. Secr. Res. Doc. 2014/008.

Jonsson B, Jonsson N. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci. 61(12):2369–2383. doi:10.1139/f04-215

Jonsson B, Jonsson N. 2009a. A review of the likely effects of climate change on anadromous Atlantic salmon (*Salmo salar*). J Fish Biol. 75:2341–2447.

Jonsson B, Jonsson N. 2009b. Restoration and enhancement of salmonid populations and habits with special reference to Atlantic salmon. Am Fish Soc Sym. 69:497–536.

Jonsson B, Jonsson N, Albretsen J. 2016. Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic. J Fish Biol. 88(2):618–637. doi:10.1111/jfb.12854

Jonsson B, Jonsson N, Hansen LH. 2003. Marine survival and growth of wild and hatchery reared Atlantic salmon. J Appl Ecol. 40(5):900–911. doi:10.1046/j.1365-2664.2003.00851.x

Jonsson N, Jonsson B, Hansen LP. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon (*Salmo salar*). J Anim Ecol. 67(5):751–762. doi:10.1046/j.1365-2656.1998.00237.x

Jordan RH, Storrs LO. 1982. The first record of the Great Auk (*Pinguinus impennis*) from Labrador. Auk. 99(1):167–168. doi:10.2307/4086034

Joyce W, Campana SE, Natanson LJ, Kohler WE, Pratt HL, Jensen JF. 2002. Analysis of the stomach contents of the porbeagle shark (*Lamna nasa* Bonneterre) in the northwest Atlantic. ICES J Mar Sci. 59(6):1263–1269. doi:10.1006/jmsc.2002.1286

Karlsson L, Karlsson O. 1994. The Baltic salmon (*Salmo salar*): its history, present situation and future. Dana. 10:61–85.

Karlsson S, Diserud OH, Fiske P, Hindar K, Grant WS. 2016. Widespread genetic introgression of escaped Atlantic salmon in wild salmon populations. ICES J Mar Sci.73(10):2488–2498. doi:10.1093/icesjms/fsw121

Kelly B, Benoît HP, Chaput G, Jones RA, Power M. 2018. Spawning-strategy-dependent diet in two North American populations of Atlantic salmon Salmo salar. J Fish Biol. 94:49–52.

Kerekes J, Schwinghamer P. 1978. Aquatic resource inventory Fundy National Park; Part 2—limnological conditions. Can. Wildl. Ser., Envir. Can. Tech. Rep. 23:143.

Keyser F, Wringe BF, Jeffery NW, Dempson JB, Duffy S, Bradbury IR. 2018. Predicting impacts of escaped farmed salmon on wild salmon populations. Can J Fish Aquat Sci. 75(4):506–512. doi:10.1139/cjfas-2017-0386

Kidokoro H, Goto T, Nagasawa T, Nishida H, Akamine T, Sakurai Y. 2010. Impact of a climate regime shift on the migration of Japanese common squid (*Todarodes pacificus*) in the Sea of Japan. ICES J Mar Sci. 67(7):1314–1322. doi:10.1093/icesjms/fsq043

Kindong R, Wang H, Wu F, Xiaojie D, Tian S. 2020. Age, growth, and sexual maturity of the crocodile shark *Pseudocarcharias kamoharae* from the eastern Atlantic Ocean. Front Mar Sci. 7:857. doi:10.3389/fmars.2020.586024

Knies J, Cabedo-Sanz P, Belt ST, Baranwal S, Fietz S, Rosell-Melé A. 2014. The emergence of modern sea ice cover in the Arctic Ocean. Nat Commun. 5:5608. doi:10.1038/ncomms6608

Kocik JF, Brown RW. 2002. From game fish to tame fish: Atlantic salmon in North America, 1798 to 1998. In: Lynch KD, Jones ML, Taylor WW, editors. Sustaining North American Salmon: perspectives across regions and disciplines. Bethesda (MD): American Fisheries Society. p. 3–31.

Korman J, Marmorek DR, Lacroix GL, Amiro PG, Ritter JA, Watt WD, Cutting RE, Robinson DCE. 1994. Development and evaluation of a biological model to assess regional-scale effects of acidification on Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci. 51(3):662–680. doi:10.1139/f94-067

Kroodsma DA, Mayorga J, Hochberg T, Miller NA, Boerder K, Ferretti F, Wilson A, Bergman B, White TD, Block BA, et al. 2018. Tracking the global footprint of fisheries. Science 359(6378):904–908. doi:10.1126/science.aao5646

Lacroix GL. 2008. Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy. Can J Fish Aquat Sci. 65(9):2063–2079. doi:10.1139/F08-119

Lacroix GL. 2013. Migratory strategies of Atlantic salmon (*Salmo salar*) postsmolts and implications for marine survival of endangered populations. Can J Fish Aquat Sci. 70(1):32–48. doi:10.1139/cjfas-2012-0270

Lacroix GL. 2014. Large pelagic predators could jeopardize the recovery of endangered Atlantic salmon. Can J Fish Aquat Sci. 71(3):343–350. doi:10.1139/cjfas-2013-0458

Lacroix GL, Knox D. 2005. Distribution of Atlantic salmon (*Salmo salar*) postsmolts of different origin in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival. Can J Fish Aquat Sci. 62(6):1363–1376. doi:10.1139/f05-055

Lajus DL, Dmitrieva ZV, Kraikovski AV, Lajus JA, Alexandrov DA. 2007. Atlantic salmon fisheries in the White and Barents Sea basins: dynamic of catches in the 17-18th century and comparison with 19-20th century data. Fish Res. 87(2-3):240–254. doi:10.1016/j.fishres.2007.07.001

Lande R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am Nat. 142(6):911–927. doi:10.1086/285580

Lauridsen R. 2019. Fisheries research review 2018: River Frome. Accessed 15/06/2020. www.gwct.org.uk/fisheriesreport.

Law R. 2000. Fishing, selection, and phenotypic evolution. ICES J Mar Sci. 57(3):659–668. doi:10.1006/jmsc.2000.0731

Leaniz CR, Martinez JJ. 1988. The Atlantic salmon in the rivers of Spain with particular reference to Cantabria. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm. p. 179–209.

Lear WH. 1972. Food and feeding of Atlantic salmon in coastal and over oceanic depths. Res Bull Intern Comm Northw Atl Fish. 9:27–39.

Lefèvre MA, Stokesbury MJW, Whoriskey FG, Dadswell MJ. 2013. Migration of Atlantic salmon smolts and post-smolts in the Riviere Saint-Jean, QC north shore from riverine to marine ecosystems. Environ Biol Fish. 96(9):1017–1028. doi:10.1007/s10641-012-0100-8

Legault CM. 2005. Population viability analysis of Atlantic salmon in Maine, USA. Trans Am Fish Soc. 134(3):549–562. doi:10.1577/T04-017.1

Lehnert SJ, Kess T, Bentzen P, Kent MP, Lien S, Gilbey J, Clement M, Jeffrey NW, Waples RS, Bradbury IR. 2019. Genomic signatures and correlates of widespread population declines in salmon. Nat Commun. 10:2996.

Lenders HJR, Chamulean TPM, Hendriks AJ, Lauwerier RCGM, Leuven RSEW, Verbek WCEP. 2016. Historic rise of waterpower initiated the collapse of salmon stocks. Sci Rep. 6:29269.

Limburg KE, Waldman JR. 2009. Dramatic declines in North Atlantic diadromous fishes. BioSci. 59(11):955–965. doi:10.1525/bio.2009.59.11.7

Link JS, Watson RA. 2019. Global ecosystem overfishing: clear delineation within real limits to production. Sci Adv. 5(6):eaav0474. doi:10.1126/sciadv.aav0474

Lothian AJ, Newton M, Barry J, Walters M, Miller RC, Adams CE. 2018. Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish River and the near-shore coastal marine environment. Ecol Freshw Fish. 27(2):549–558. doi:10.1111/eff.12369

Louca S, Doebeli M. 2015. Detecting cyclicity in ecological time series. Ecology. 96(6):1724–1732. doi:10.1890/14-0126.1

Makhrov AA, Verspoor E, Artamonova VS, O'Sullivan M. 2005. Atlantic salmon colonization of the Russian Arctic coast: pioneers from North America. J Fish Biol. 67(s1):68–79. doi:10.1111/j.0022-1112.2005.00840.x

Mancini A, Senko J, Borquez-Reyes R, Póo JG, Seminoff JA, Koch V. 2011. To poach or not to poach an endangered species: elucidating the economic and social drivers behind illegal sea turtle hunting in Baja California Sur, Mexico. Hum Ecol. 39(6):743–756. doi:10.1007/s10745-011-9425-8

Marshall L. 1994. Trapping and trucking Atlantic salmon on the Saint John River. In: Calabi S, Stout A, editors. A Hard Look at Some Tough Issues: Proceedings of the New England Atlantic Salmon Management Conference. Newburyport (MA): Atlantic Salmon Association. p. 158–169.

Mather FJ, Jones LM, Jones AG. 1995. Historical document: life history and fisheries of Atlantic bluefin tuna. US Dep. Comm., NOAA, NMFS, Southeast Fish. Sci. Center 370.

Mawle GW. 1991. Restoration of the River Taff, Wales. In: Mills D, editor. Strategies for the rehabilitation of salmon rivers. London (UK): Linnean Society. p.109–121.

Mawle GW, Milner NJ. 2003. The return of salmon to cleaner rivers – England and Wales. In: Mills D, editor. Salmon at the edge. Oxford (UK): Blackwell Science. p. 186–199.

McDermott T. 1996. Screebe: historical review of angling records from a salmonid fishery in the west of Ireland (1865-1995). Available from ScreebeWorkshop@Marine.ie.

McGinnity P, Ferguson A, Baker N, Cotter D, Cross T, Cooke D, Hynes R, O'Hea B, O'Maoiléidigh N, Prodöhl P, et al. 2003. A two-generation experiment comparing the fitness and life-history traits of native, ranched, non-native, farmed and hybrid Atlantic salmon under natural conditions. In: Mills D, editor. Salmon at the edge. Oxford (UK): Blackwell Science. p. 138–143.

McKinnell S, Trudel M. 2014. SALOSIS (Salmon Ocean Surveillance Information System). N. Pac. Anad. Fish. Comm. Doc. Fish. Oceans Can. 1524.

Middlemas SJ, Armstrong JD, Thompson PM. 2003. The significance of marine mammal predation on salmon and sea trout. In: Mills D, editor. Salmon at the edge. Oxford (UK): Blackwell Science. p. 43–60.

Miller KM, Teffer A, Tucker S, Li S, Schulze AD, Trudel M, Juanes F, Tabata A, Kaukinen KH, Ginther NG, et al. 2014. Infectious diseases, shifting climates and opportunistic predators: cumulative factors potentially impacting wild salmon declines. Evol Appl. 7(7):812–855. doi:10.1111/eva.12164

Miller NA, Roan A, Hochberg T, Amos J, Kroodsma DA. 2018. Identifying global patterns of transshipment behavior. Front Mar Sci. 5:240.

Mills D. 1989. Ecology and management of Atlantic salmon. London (UK): Chapman and Hall.

Mills D. 1991. Strategies for the rehabilitation of salmon rivers. London (UK): Linnean Society.

Mills D. 1993. Control of marine exploitation. In: Mills D, editor. Salmon in the Sea and new enhancement strategies. Oxford (UK): Fishing News Books. p. 233–248.

Mills KE, Pershing AJ, Sheehan TF, Mountain D. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. Glob Change Biol. 19(10):3046–3061. doi:10.1111/gcb.12298

Montevecchi WA, Cairns DK, Myers RA. 2002. Predation on marine phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the Northwest Atlantic. Can J Fish Aquat Sci. 59(4):602–571. doi:10.1139/f02-033

Montevecchi WA, Cairns DK. 2003. Predation on post-smolt Atlantic salmon by gannets: research implications and opportunities. In: Mills D, editor. Salmon at the edge. Oxford (UK): Blackwell Science. p. 61–77.

Moore A, Waring CP. 1996. Sublethal effects of the pesticide Diazinon on olfactory function in mature, male Atlantic salmon parr. J. Fish Biol. 48(4):758–775. doi:10.1111/j.1095-8649.1996.tb01470.x

Myers RA, Hutchings JA, Barrowman NJ. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol Appl. 7(1):91–106. doi:10.1890/1051-0761(1997)007[0091:WDFSCT] 2.0.CO;2]

Myers RA, Mertz G, Bridson JA, Bradford MJ. 1998. Simple dynamics underlie sockeye salmon (*Oncorhynchus nerka*) cycles. Can J Fish Aquat Sci. 55(10):2355–2364. doi:10.1139/f98-059

Nagasawa K. 1998. Predation by salmon shark (*Lamna ditropis*) on Pacific salmon. (*Onchorhychus* spp.) in the North Pacific Ocean. N Pac Anad Fish Comm Bull. 1:419–433.

NASCO (North Atlantic Salmon Conservation Organization). 2019. State of North Atlantic Salmon. Accessed 12/12/2019. www.nasco.int/pdf/iys/SoS-final-online.pdf.

Netboy A. 1980. Salmon, the World's Most Harassed Fish. London (UK): André Deutsch Ltd. p. 304.

Nicola G, Elvira B, Jonsson B, Ayllón D, Almodóvar A. 2018. Local and climatic drivers of Atlantic salmon decline in southern Europe. Fish Res. 198:78–85. doi:10.1016/j.fishres.2017.10.012

Nielsen JL, Ruggerone JL, Zimmerman CE. 2013. Adaptive strategies and life history characteristics of a warming climate: salmon in the arctic. Environ Biol Fish. 96(10-11):1187–12206. doi:10.1007/s10641-012-0082-6

Niemelä E, Erkinaro J, Dempson JB, Julkunen M, Zubchenko A, Prusov S, Svenning MA, Ingvaldsen R, Holm M, Hassinen E. 2004. Temporal synchrony and variation in abundance of Atlantic salmon (*Salmo salar*) in two subarctic Barents Sea rivers: influence of oceanic conditions. Can J Fish Aquat Sci. 61(12):2384–2391. doi:10.1139/f04-208

Nislow KH, Sepulveda AJ, Folt C. 2004. Mechanistic linkage of hydrologic regime to summer growth of age-0 Atlantic salmon. Trans Am Fish Soc. 133(1):79–88. doi:10.1577/T02-168

Niven A, McCauley M, Scott R. 2016. Foyle area and tributaries catchment status report 2015. Loughs Agency Foyle Carlingford Irish Lights Comm. 16 LA/CSR/F/.

Norway Map. 2017. Norway's top Atlantic salmon fishing rivers. Accessed 13/12/2019. www.norway.bendiksen.org/map.salmon.php.

NRC (National Research Council USA). 2004. Atlantic Salmon in Maine. Washington (DC): The National Academic Press. p. 236.

NRW (Natural Resources Wales). 2019. Salmon and sea trout stocks in Wales. www.naturalresources.wales.

Nyberg-Kallio I, Saloniemi I, Koljonen M-L. 2020. Increasing temperature associated with increasing grilse proportion and smaller grilse-size of Atlantic salmon. J Appl Ichthyol. 36(3):288–297. doi:10.1111/jai.14033

Obradovich SG, Carruthers EH, Rose GA. 2014. Bottom-up limits to Newfoundland capelin (*Mallotus villosus*) rebuilding: the euphasiid hypothesis. ICES J Mar Sci. 71(4):775–783. doi:10.1093/icesjms/fst184

O'Connell MF, Bourgeois CE. 1987. Atlantic salmon enhancement in the Exploits River, Newfoundland, 1957-1984. N Am J Fish Manag. 7(2):207–214. doi:10.1577/1548-8659(1987)7<207:ASEITE > 2.0.CO;2

O'Connell MF, Dempson JB, Reddin DG. 1992. Evaluation of the impacts of major management changes in the Atlantic salmon (*Salmo salar* L.) fisheries of Newfoundland and Labrador, Canada, 1984-1988. ICES J Mar Sci. 49(1):69–87. doi:10.1093/icesjms/49.1.69

Olafsson K, Einarsson SM, Gilbey J, Pompoulie C, Gudmundur O, Hreggridsson GO, Hjorliefsdottir S, Gudjonsson S. 2016. Origin of Atlantic salmon (*Salmo salar*) at sea in Icelandic waters. ICES J Mar Sci. 73(6):1525–1532. doi:10.1093/icesjms/fsv176

Olmos M, Massiot-Granier F, Prévost E, Chaput G, Bradbury IR, Nevoux M, Rivot E. 2019. Evidence for special coherence in time trends of marine life history traits of Atlantic salmon in the North Atlantic. Fish Fish. 20(2):322–342. doi:10.1111/faf.12345

Olmos M, Payne MR, Nevoux M, Prévost E, Chaput G, Du Pontavice H, Guitton J, Sheehan T, Mills K, Rivot E. 2020. Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. Glob Chang Biol. 26(3):1319–1337. doi:10.1111/gcb.14913

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428(6986):932–935. doi:10.1038/nature02430

Olson SL, Swift CC, Mokhiber C. 1979. An attempt to determine the prey of the Great Auk (*Pinquinus impennis*). Auk. 94:790–792.

Ó Maoiléidigh N, White J, Hansen LP, Potter T, Russell I, Reddin D, Sheehan T. 2018. Fifty years of marine tag recoveries from Atlantic salmon. ICES Coop Res Rep. 343: 121. doi:10.17895/ices.pub.4542

Otero J, Jensen AJ, L'Abée-Lund JH, Stenseth NC, Storvik GO, Vøllestad LA. 2011. Quantifying the ocean, freshwater and human effects on year-to-year variability of one-sea-winter Atlantic salmon angled in multiple Norwegian rivers. PLoS One. 6(8):e24005. doi:10.1371/journal.pone.0024005

Paloheimo JE, Elson PF. 1974a. Reduction of Atlantic salmon (*Salmo salar*) caught in Canada attributed to the Greenland fishery. J Fish Res Bd Can. 31(9):1467–1480. doi:10.1139/f74-176

Paloheimo JE, Elson PF. 1974b. Effects of the Greenland fishery for Atlantic salmon on Canadian stocks. Intern Atl Sal Found Spec Pub Ser. 5:1–34.

Park J, Lee J, Seto K, Hochberg T, Wong BA, Miller NA, Takasaki K, Kubota H, Oozeki Y, Doshi S, et al. 2020. Illuminating dark fishing fleets in North Korea. Sci Adv. 6(30):eabb119. doi:10.1126/sciadv.abb1197

Parrish DL, Behnke RJ, Gephard SR, McCormick SD, Reeves GH. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)?Can J Fish Aquat Sci. 55(S1):281–287. doi:10.1139/d98-012

Pasanen L, Laukkanen-Nevala P, Launonen I, Prusov S, Holmström L, Niemelä E, Erkinaro J. 2017. Extraction of sea temperature in the Barents Sea by a scale space multiresolution method-prospects for Atlantic salmon. J Statist. 44(13):2317–2336. doi:10.1080/02664763.2016.1252731

Payne MR, Egan A, Fässler SMM, Hátún H, Holst JC, Jacobsen JA, Slotte A, Loeng H. 2012. The rise and fall of the northeast Atlantic blue whiting (*Micromesistius poutassau*. Mar Biol Res. 8(5-6):475–487. doi:10.1080/17451000.2011.639778

Perez J, Izquierdo JL, Hoz J, Garcia-Vazquez E. 2005. Female biased angling harvests of Atlantic salmon in Spain. Fish Res.74(1-3):127–133. doi:10.1016/j.fishres.2005.03.008

Peyronnet A, Friedland KD, Maoiléidigh NÓ. 2008. Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon (*Salmo salar*) in the northeast Atlantic Ocean. J Fish Biol. 73(4):945–962. doi:10.1111/j.1095-8649.2008.01984.x

Potter ECE, Crozier WW. 2000. A perspective on the marine survival of Atlantic salmon. In: Mills D, editor. The Ocean Life of Atlantic salmon: environmental and biological factors influencing survival. Oxford, UK: Blackwell Science, p. 19–36.

Potter ECE, Crozier WW, Schön PJ, Nicholson MD, Maxwell DL, Prévost E, Erkinaro J, Gudbergsson G, Karlsson L, Hansen LP, et al. 2004. Estimating and forecasting pre-fishery abundance of Atlantic salmon (*Salmo salar*) in the northwest Atlantic for the management of mixed-stock fisheries. ICES J Mar Sci. 61(8):1359–1369. doi:10.1016/j.icesjms.2004.08.012

Potter ECE, Dunkley DA. 1993. Evaluation of marine exploitation of salmon in Europe. In: Mills D, editors. Salmon in the Sea and new enhancement strategies. Oxford (UK): Fishing News Books. p. 203–219.

Pramod G, Nakamura K, Pitcher TJ, Delagran L. 2014. Estimates of illegal and unreported fish in seafood imports to the USA. Mar Pol. 48:102–113. doi:10.1016/j.marpol.2014.03.019

Radchenko VI. 2020. IUU fishing indicators and warnings: how to organize information collection and dissemination. N Pac Fish Comm Newsl. 48:11–25.

Reddin DG. 1988. Ocean life of Atlantic salmon (*Salmo salar* L.) in the northwest Atlantic. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm. p. 483–511.

Reddin DG, Friedland KD. 1999. A history of identification to continent of origin of Atlantic salmon (*Salmo salar* L.) at west Greenland, 1969-1997. Fish. Res.43(1-3):221–235. doi:10.1016/S0165-7836(99)00074-0

Reddin DG, Hansen LP, Bakkestuen V, Russell I, White J, Potter ECE, Dempson JB, Sheehan TF, Ó Maoiléidigh N, Smith GW, Isaksson A, et al. 2012. Distribution and biological characteristics of Atlantic salmon (*Salmo salar*) at Greenland based on the analysis of historical tag recoveries. ICES J Mar Sci. 69(9):1589–1597. doi:10.1093/icesjms/fss087

Reddin DG, Helbig J, Thomas A, Whitehouse BG, Friedland KD. 2000. Survival of Atlantic salmon (*Salmo salar* L.) related to marine climate. In: Mills D, editor. The ocean life of Atlantic Salmon: environmental and biological factors influencing survival. Oxford (UK): Fishing News Books. p. 88–91.

Reddin DG, Shearer WM. 1987. Sea-surface temperature and distribution of Atlantic salmon in the Northwest Atlantic Ocean. Am Fish Soc Sym. 1(1987):262–275.

Renkawitz MD, Sheehan TE, Dixon HJ, Nygaard R. 2015. Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. Mar Ecol Prog Ser. 538:197–211. doi:10.3354/meps11470

Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. Bull Fish Res Bd Can. 191:382.

Rikardsen AH, Hansen LP, Jensen AJ, Vollen T, Finstad B. 2008. Do Norwegian salmon feed in the northern Barents Sea?J Fish Biol. 72(7):1792–1798. doi:10.1111/j.1095-8649.2008.01823.x

Ritter JA. 1997. The contribution of Atlantic salmon (*Salmo salar* L.) enhancement to a sustainable resource. ICES J Mar Sci. 54(6):1177–1187. doi:10.1016/S1054-3139(97)80025-2

Rodríguez JP, Fernández-Gracia J, Duarte CM, Irigoien X, Eguíluz VM. 2021. The global network of ports supporting high seas fishing. Sci Adv. 7(9):eabe3470. doi:10.1126/sciadv.abe3470

Rosenthal E. 2008. Europe's appetite for seafood propels illegal trade. *New York Times*, January 15, New York.

Rub AMJ, Stamford BP. 2020. Evidence of a 'dinner bell' effect from acoustic transmitters in adult Chinock salmon. Mar Ecol Prog Ser. 641:1–11.

Ruggerone GT, Irvine JR. 2018. Numbers and biomass of natural- and hatchery- origin Pink salmon, Chum salmon and Sockeye salmon in the North Pacific Ocean, 1925-2015. Mar Coast Fish. 10(2):152–168. doi:10.1002/mcf2.10023

Russell I, Aprahamian M, Barry J, Davidson I, Fiske P, Ibbotson A, Kennedy R, MacLean J, Moore A, Otero J, et al. 2012. The influence of the freshwater environment and biological characteristics of Atlantic salmon smolts on their subsequent marine survival. ICES J Mar Sci. 69(9):1563–1573. doi:10.1093/icesjms/fsr208

Rybicki S, Hamon KG, Simons S, Temming A. 2020. To fish or not to fish-economic perspectives of the pelagic Northeast Atlantic mackerel and herring fishery. Front Mar Sci. 7:675. doi:10.3389/fmars.2020.00675

Säisä M, Koljonen M-L, Gross R, Nilsson J, Tähtinen J, Koskiniemi J, Vasemägi A. 2005. Population genetic structure and postglacial colonization of Atlantic salmon (*Salmo salar*) in the Baltic Sea area based on microsatellite DNA variation. Can J Fish Aquat Sci. 62(8):1887–1904. doi:10.1139/f05-094

Sackton J. 2018. Chinese crackdown on salmon smuggled through Vietnam in nation-wide raids. Seafoodnews.com, April 5. Accessed 15/04/2020. www.tinyur/com.iy7c7ms2l.

Sandal D. 2006. The rise and decline of blue whiting fisheries – capacity expansion and future regulations. Mar Pol. 30:315–327.

Saunders RL, Sprague JB. 1967. Effects of copper-zinc mining pollution on a spawning migration of Atlantic salmon. Wat Res. 1(6):419–432. doi:10.1016/0043-1354(67)90051-6

Scarnecchia DL. 1984. Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci. 41(6):917–935. doi:10.1139/f84-107

Scarnecchia DL, Isaksson A, White SE. 1991. Effects of the Faroese long-line fishery, other oceanic fisheries and oceanic variations on age of maturity of Icelandic north-coast stocks of Atlantic salmon (*Salmo salar*). Fish Res. 10(3-4):207–228. doi:10.1016/0165-7836(91)90076-R

Schwartzlose RA, Alheit J, Bakun A, Baumgartner TR, Cloete R, Crawford RJM, Fletcher WJ, Green-Ruiz Y, Hagen E, Kawasaki T, et al. 1999. World-wide, large- scale fluctuations of sardine and anchovy populations. S Afr J Mar Sci. 21(1):289–347. doi:10.2989/025776199784125962

Scruton DA, Pennell CJ, Bourgeois CE, Goosney RF, King L, Booth RK, Eddy W, Porter JR, Ollerhead LMN, Clarke KD. 2008. Hydroelectricity and fish: a synopsis of comprehensive studies of upstream and downstream passage of anadromous, wild Atlantic salmon, *Salmo salar*, on the Exploits River, Canada. Hydrobiologia. 609(1):225–239. doi:10.1007/s10750-008-9410-4

Seitz AC, Courtney MB, Evans MD, Manishin K. 2019. Pop-up archival tags reveal evidence of intense predation on large immature Chinook salmon (*Onchorhynchus tshawytscha*) in the North Pacific Ocean. Can J Fish Aquat Sci. 76(9):1608–1615. doi:10.1139/cjfas-2018-0490

Shearer WM. 1988. Relating catch records to stocks. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm. p. 256–274.

Shearer WM. 1992. The Atlantic salmon: natural history, exploitation, and future management. Oxford (UK): Fishing News Books. p. 244.

Sheehan T. 2017. Overview of the current west Greenland Atlantic salmon sampling program. Accessed 10/02/2021. www.nefsc.noaa.gov/publications.

Sheehan T. 2019. Current status of knowledge, data, and research efforts on Atlantic salmon at Greenland: what do we have, what do we need, and what should we do moving forward. US Depart. Commerce, Northeast Fish. Sci. Cen. Ref. Doc. 19-10.

Sinclair M, Power M, Head E, William KWL, McMahon M, Mohn R, O'Boyle R, Swain D, Tremblay JI. 2015. Eastern Scotian Shelf trophic dynamics: a review of the evidence for diverse hypotheses. Prog Ocean. 138:305–321. doi:10.1016/j.pocean.2015.09.005

Sinnatamby RN, Dempson JB, Chaput G, Caron F, Niemelä E, Erkinaro J, Power M. 2009. Spatial and temporal variability in the trophic ecology of Atlantic salmon in the North Atlantic inferred from analyses of stable isotope signatures. Am Fish Soc Sym. 69:447–463.

Skjelkvåle BL, Evans C, Larssen T, Hindar A, Raddum GG. 2003. Recovery from acidification in European surface waters: a view to the future. Ambio 32(3):170–175. doi:10.1579/0044-7447-32.3.170

Skilbrei OT, Wennevik V. 2006. The use of catch statistics to monitor the abundance of escaped farmed salmon and rainbow trout in the sea. ICES J Mar Sci. 63(7):1190–1200. doi:10.1016/j.icesjms.2006.05.005

Skilbrei OJ, Heino M, Svåsand T. 2015. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. ICES J Mar Sci. 72(2):670–685. doi:10.1093/icesjms/fsu133

Skomal G, Marshall H, Galuardi B, Natanson L, Braun C, Bernal D. 2021. Horizontal and vertical movement patterns and habitat use of juvenile porbeagles (*Lamna nasus*) in the western North Atlantic. Front Mar Sci. 8:16. doi:10.3389/fmars.2021.624158

Smith CH, Davis JM. 1981. A spatial analysis of wildlife's ten-year cycle. J Biogeogr. 8(1):27–35. doi:10.2307/2844590

Soberón JA. 2019. Grinnellian niche perspective on species-area relationships. Am Nat. 194(6):760–775. doi:10.1086/705898

Søreide JE, Hop H, Carrol ML, Falk-Petersen S, Hegseth EN. 2006. Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Ocean. 71(1):59–87. doi:10.1016/j.pocean.2006.06.001

Soto DX, Trueman CN, Samways KM, Dadswell MJ, Cunjak RA. 2018. Ocean warming cannot explain synchronous declines in North American Atlantic salmon populations. Mar Ecol Prog Ser. 601:203–213. doi:10.3354/meps12674

Souza ENd, Boerder K, Matwin S, Worm B. 2016. Improving pattern detection from satellite AIS using data mining and machine learning. PLoS One. 11(7):e0158248. doi:10.1371/journal.pone.0158248

Spares AD, Dadswell MJ, Dickinson MP, Stokesbury MJW. 2015. Mastery of the marine environment: a critical review of anadromous Salmonidae. Rev Fish Biol Fisheries. 25(3):503–509. doi:10.1007/s11160-015-9392-z

Spares AD, Reader JM, Stokesbury MJW, McDermott T, Zikovsky L, Avery TS, Dadswell MJ. 2007. Inferring marine distribution of Canadian and Irish Atlantic salmon (*Salmo salar* L.) in the North Atlantic Ocean from tissue concentrations of caesium-137. ICES J Mar Sci. 64(2):394–404. doi:10.1093/icesjms/fsl040

Stansbury AL, Götz T, Deecke VB, Janik VM. 2014. Grey seals use antropogenic signals from acoustic tags to locate fish: evidence from a simulated foraging task. Proc R Soc B 282:1798.

Stenson GB, Haug T, Hammill MO. 2020. Harp seals: monitors of change in differing ecosystems. Front Mar Sci. 7:738. doi:10.33889/fmars.2020.569258

Stich DS, Zydlewski GB, Kocik JF, Zydlewski JD. 2015. Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. Mar Coast Fish. 7(1):68–86. doi:10.1080/19425120.2015.1007185

Stokesbury MJ, Lacroix G, Dadswell MJ, Price EL, Knox D. 2001. Identification by scale analysis of farmed Atlantic salmon juveniles in S. W. New Brunswick rivers. Trans Am Fish Soc. 130(5):815–822. doi:10.1577/1548-8659(2001)130<0815:IBSAOF > 2.0.CO;2

Stokesbury MJW, Dadswell MJ, Holland KI, Jackson RD, Bowen D, O'Dor RK. 2009. A review of future methods for tracking of anadromous fishes using hybrid acoustic and archival tags. Am Fish Soc Sym. 69:311–320.

Strøm JF, Rikardsen AH, Campana SE, Righton D, Carr J, Aarestrup K, Stokesbury MJW, Gargan P, Javierre PC, Thorstad EB. 2019. Ocean predation and mortality of adult Atlantic salmon. Sci Rep. 9(1):7890. doi:10.1038/s41598-019-44041-5

Strøm JF, Thorstad EB, Chafe G, Sørbye SH, Righton D, Rikardsen AH, Carr J. 2017. Ocean migration of pop-up satellite tagged Atlantic salmon from the Miramichi River in Canada. ICES J Mar Sci. 74(5):1356–1370. doi:10.1093/icesjms/fsw220

Strøm JF, Thorstad EB, Hedger RD, Rikardsen AH. 2018. Revealing the full ocean migration of individual Atlantic salmon. Anim Biotel. 6:2. doi:10.1186/s40317-018- 0146-2

Strøm JF, Thorstad ED, Rikardsen AH. 2020. Thermal habitat of adult Atlantic salmon *Salmo salar* in a warming ocean. J Fish Biol. 96(2):327–336. doi:10.1111/jfb.14187

Taguchi K. 1957. The seasonal variation of the good fishing area of salmon and the movement of water masses in the waters of the western North Pacific-II. The distribution and migration of salmon populations in offshore waters. Jap Soc Sci Fish. 22(9):515–521. doi:10.2331/suisan.22.515

Takahashi M, Watanabe Y, Yatsu A, Nishida H. 2009. Contrasting responses in larval and juvenile growth to a climate-ocean regime shift between anchovy and sardine. Can J Fish Aquat Sci. 66(6):972–982. doi:10.1139/F09-051

Taylor VR, Bauld BR. 1973. A program for increased Atlantic salmon (*Salmo salar*) production on a major Newfoundland river. In: Smith MW, Carter WM, editors. Proceedings of the International Symposium on the Atlantic Salmon: management, biology, and survival of the species. Fredericton (NB): Unipress. p. 339–348.

Telesetsky A. 2015. Laundering fish in the global undercurrents: illegal, unreported, and unregulated fishing and transnational organized crime. Ecol Law Q. 41:939–997.

Templeman W. 1967. Atlantic salmon from the Labrador Sea and off West Greenland, taken during A.T. Cameron cruise, July-August 1965. Intern Comm N W Atl Fish Res Bull. 4:5–40.

Templeman W. 1968. Distribution and characteristics of Atlantic salmon over oceanic depths and on the bank and shelf slope areas off Newfoundland, March-May. 1966. Intern Comm N W Atl Fish Res Bull. 5:62–68.

The Times of London. 1967. The Times Atlas of the World. Boston (MA): Houghton Mifflin. p. 272.

Thorstad EB, Fleming IA, McGinnity P, Soto D, Wennevik V, Whorisky F. 2008. Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature. Norw Ins Nat Res Spec Rep. 36:1–114.

Thorstad EB, Whoriskey F, Uglem I, Moore A, Rikardsen AH, Finstad B. 2012. A critical life stage of the Atlantic salmon (*Salmo salar*): behaviour and survival during the smolt and initial post-smolt migration. J Fish Biol. 81(2):500–542. doi:10.1111/j.1095-8649.2012.03370.x

Tiews K. 1978. On the disappearance of bluefin tuna in the North Sea and its ecological implications for herring and mackerel. Rap Proc-v Réun Con Intern Explor Mer. 172:301–309.

Tingley MW, Monahan WB, Beissinger SR, Moritz C. 2009. Birds track their Grinnellian niche through a century of climate change. Proc Nat Acad Sci USA. 106(Supplement_2):19637–19643. doi:10.1073/pnas.0901562106

Todd CD, Hughes SL, Marshall CT, MacLean JC, Lonergan ME, Biuw EM. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. Glob Change Biol. 14(5):958–970. doi:10.1111/j.1365-2486.2007.01522.x

Trueman CN, MacKenzie KM, Palmer MR. 2012. Stable isotopes reveal linkages between ocean climate, plankton community dynamics and survival of two populations of Atlantic salmon (*Salmo salar*). ICES J Mar Sci. 69(5):784–794. doi:10.1093/icesjms/fss066

Tucker S, Hipfner JM, Trudel M. 2016. Size and condition dependent predation: a seabird disportionately targets substandard individual juvenile salmon. Ecology. 97(2):461–471. doi:10.1890/15-0564.1

Tucker S, Pazzia I, Rowan D, Rasmussen JE. 1999. Detecting pan-Atlantic migration in salmon (*Salmo salar*) using ^{137}Cs. Can J Fish Aquat Sci. 56(12):2235–2239. doi:10.1139/f99-267

Turrell WR, Shelton TGJ. 1993. Climatic change in the north-eastern Atlantic and its impacts on salmon stocks. In: Mills D, editor. Salmon in the Sea and new enhancement strategies. Oxford (UK): Fishing News Books. p. 40–78.

Utne KR, Thomas K, Jacobsen JA, Johanna F, Maoiléidigh NÓ, Broms CT, Melle W. 2021. Feeding interactions between Atlantic salmon (*Salmo salar*) postsmolts and other planktivorous fish in the Northeast Atlantic. Can J Fish Aquat Sci. 78(3):255–268. doi:10.1139/cjfas-2020-0037

Verspoor E, Knox D, Marshall S. 2016. Assessment of interbreeding and introgression of farm genes into a small Scottish Atlantic salmon (*Salmo salar*) stock: ad hoc samples and ad hoc results?J Fish Biol. 89(6):2680–2696. doi:10.1111/jfb.13173

Verspoor E, O'Sullivan M, Arnold AL, Knox D, Amiro PG. 2002. Restricted matrilineal gene flow and regional differentiation among Atlantic salmon (*Salmo salar* L.) populations within the Bay of Fundy, eastern Canada. Heredity. 89(6):465–472. doi:10.1038/sj.hdy.6800166

Vester H, Hammerschmidt K. 2013. First record of killer whales (*Orcinus orcas*) feeding on Atlantic salmon (*Salmo salar*) in northern Norway suggest a multi-prey feeding type. Mar Biodiver Rec. 6:e9. doi:10.1017/S1755267212001030

Vigfússon O, Ingólfsson A. 1993. Quota purchase. In: Mills D, editor. Salmon in the Sea and new enhancement strategies. Oxford (UK): Blackwell Science. p. 249–266.

Vollset KW, Krontveit RI, Jansen PA, Finstad B, Barlaup BT, Skilbrei OT, Krkošek M, Romunstad P, Aunsmo A, Jensen AJ, et al. 2016. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish Fish. 17(3):714–730. doi:10.1111/faf.12141

Walters CJ, Collie JS. 1988. Is research on environmental factors useful to fisheries management. Can J Fish Aquat Sci. 45(10):1848–1854. doi:10.1139/f88-217

Watanabe Y, Zenitani H, Kimura R. 1995. Population declines of the Japanese sardine *Sardinops melanostictis* owing to recruitment failures. Can J Fish Aquat Sci. 52(8):1609–1616. doi:10.1139/f95-154

Watt WD. 1987. A summary of the impact of acid rain on Atlantic salmon (*Salmo salar*) in Canada. Water Air Soil Pollut. 35(1-2):27–35. doi:10.1007/BF00183841

Weimerskirch H, Collet J, Corbeau A, Pajot A, Hoaran F, Marteau C, Filippi D, Patrick SC. 2020. Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of nondeclared fishing. Proc Nat Acad Sci USA. 117:3006–3014. doi:10.1073/pnas.1915499117

Weitkamp LA, Goulette G, Hawkes J, O'Malley M, Lipsky C. 2014. Juvenile salmon in estuaries: comparisons between North American and Pacific salmon populations. Rev Fish Biol Fisheries. 24(3):713–736. doi:10.1007/s11160-014-9345-y

Wells BK, Field JC, Thayer JA, Grimes CB, Bograd SJ, Sydeman WJ, Schwing FB, Hewitt HR. 2008. Untangling the relationships among climate, prey and predators in an ocean ecosystem. Mar Ecol Prog Ser. 364:15–29. doi:10.3354/meps07486

Wheeler A, Gardner D. 1974. Survey of the literature of marine predators on salmon in the north-east Atlantic. Aquacult Res. 5(3):63–66. doi:10.1111/j.1365-2109.1974.tb01213.x

Whitehead A. 2003. Progress in ending mixed-stock interceptor fisheries: United Kingdom. In: Mills D, editor. Salmon at the edge. Oxford (UK): Blackwell Science. p. 78–83.

Whitfield CJ, Aherne J, Watmough SA, Dillon PJ, Clair TA. 2006. Recovery from acidification in Nova Scotia: temporal trends and critical loads for 20 headwater lakes. Can J Fish Aquat Sci. 63(7):1504–1514. doi:10.1139/f06-053

Windsor ML, Hutchinson P. 1988. International cooperation through NASCO. In: Mills D, Piggins D, editors. Atlantic Salmon: planning for the future. London (UK): Croom Helm, p. 1–11.

Windsor ML, Hutchinson P. 1994. International management of Atlantic salmon, *Salmo salar* L., by the North Atlantic Salmon Conservation Organization, 1984-1994. Fish Manag Ecol. 1(1):31–44. doi:10.1111/j.1365-2400.1970.tb00004.x

Witbooi E, Ali K-D, Santosa MA, Hurley G, Husein Y, Maharaj S, Okafor-Yarwood I, Quiroz IA, Salas O. 2020. Organized crime in the fisheries sector threatens sustainable ocean economy. Nature. 588(7836):48–56. doi:10.1038/s41586-2020-2913-5

Worm B. 2016. Averting a global fisheries disaster. Proc Nat Acad Sci USA. 113:4895–4897. doi:10.1073/pnas.1604008113

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halprin BS, Jackson JBC, Lotze HK. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790. doi:10.1126/science.1132294

Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber SH. 2013. Global catches, exploitation rates, and rebuilding options for sharks. Mar Pol. 40:194–204. doi:10.1016/j.marpol.2012.12.034

Wringe BF, Jeffrey NW, Stanley RRE, Hamilton LC, Anderson EC, Fleming IA, Grant C, Dempson JB, Veinott G, Bradbury IR. 2018. Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Comm Biol. 1:108.

Yablokov AV. 1994. Validity of whaling data. Nature 367(6459):108–108. doi:10.1038/367108a0

Yokawa H, Uozumi Y. 2001. Analysis of operation patterns of Japanese longliners in the tropical Atlantic Ocean and their blue marlin catch. ICCAT Coll Vol Sci Pap. 53:318–336.

Yorwood I, Quinoz A, Salas O. 2020. Organized crime in the fisheries sector. Nature 588(7836):48–56. doi:10.1038/s41586-2020-2913-5

Zubchenko AV, Sharov F. 1993. Salmon rivers in the Kola Peninsula. Status of Atlantic salmon stocks. ICES C.M1993 /M:54.